The Value of Conserving

GENETIC RESOURCES

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. administration.

Library of Congress Cataloging in Publication Data

Oldfield, Margery L.
The value of conserving genetic resources.

Bibliography: p.
Includes index.
Supt. of Docs. no.: I 29.2:G28/2
1. Germplasm resources. 2. Germplasm resources--Economic aspects. I. Title. II. Title: Genetic resources.
S494.3.043 1984 631.5'2 84-600012

The Value of Conserving
GENETIC RESOURCES

BY
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U.S. Department of the Interior
National Park Service
Washington, D.C.
1984

Foreword

I write this foreword with the aid of an immensely helpful machine, but with a name—word processor—demeaning to the use of language. It is somewhat deceptive in that it helps me to write more efficiently but not with better quality. The machine and I are in a modern office, air conditioned and with windows sealed except to those with a special key. Most of the contents of the office are not natural products.

Yet this sense of isolation from the natural world, which is to be found where a large fraction of humanity work and play, is as much an illusion as the notion that a word-processor can transform me into a Milton. Our agriculture, so developed that it expends multiple calories of energy, mostly from fossil fuels, for each calorie of food it yields for our tables, continues, nonetheless, to depend on wild resources. Technology notwithstanding, agriculture remains a genetic dynamic. Most recently for example, a wild relative of the potato *(Solanum berthaultii)* from Peru has, because of the sticky nature of its leaves, brought the promise of improved yield and profit to Long Island potato farmers several thousands of miles to the north. Incorporating its stickiness will make life miserable for the potato beetle. While trivial in terms of calories and nutrition, gourmets still swoon over gnarled fungi from roots of oaks in the south of France and northern Italy—the black and white truffles.

When we are sick we sometimes depend very heavily on resources only recently derived from the wild, or taken directly from it. Pharmaceutical companies lust after soil samples from remote corners of the world, in the hope, realized with regularity, that they will contain a microbe with an important new antibiotic. Antibiotics derived from wild resources made a significant contribution to the Allied war effort in the Second World War. Hundreds of thousands of people in the United States are alive today because of medicines originally derived from the tropical forests, or still harvested, like curare, directly from the tropical wilds.

Yet the average citizen of an industrialized society is both ignorant and oblivious of the enormous number of ways in which we draw on wild resources, and equally oblivious of how rapidly these resouces are being eradicated from the face of the earth. In our industrialized agriculture, the pressures lead toward genetic uniformity, often with greater yield but with accompanying increases in vulnerability. In the

wild, especially in the tropics, species, by the bunch, are being rushed to extinction. It is almost as if our species was intent on constructing the biological equivalent of a black hole into which will disappear a major portion of the wonderful and useful diversity of life on earth.

No one who reads the pages that follow will fail to gain an appreciation of how intimately human existence really is intertwined with wild genetic resources. Ms. Oldfield's volume is an important compendium of ways in which human society draws directly on wild species. In their natural communities wild plants and animals also make important contributions to our lives through processes which are the joint products of the constituent species. The earth's natural ecosystems are intimately involved in how energy, water and nutrients both flow and are stored on this planet. The impoverishment of those ecosystems by extermination of their constituent parts impairs their ability to serve us through process.

The loss of diversity impairs as well our ability to probe living systems and their workings, when, for us as living entities, the science of life, biology, would seem an entirely indispensable branch of knowledge. It is a tremendous irony that the century which has produced the greatest amount of biological discovery including thrilling insights into genetic processes, is also the one which is so busy destroying so much of the evidence before it is even examined.

As a consequence, those of us who toil in the field of conservation today, are utterly convinced of the essential importance of conservation to the welfare of society. True, the enrichment inherent in a wilderness experience is also something to be cherished, and is a justification for conservation in its own right. Indeed the basic attraction to and fascination with other forms of life as well as to natural places is not in the least surprising. It is fundamentally adaptive.

A large part of the problem is that, in our isolation, it is easy to forget (if, in fact, we ever were aware) these unavoidable links with the only known living part of the universe here on Earth. With a distaste for bad news, it is an easy temptation to believe that technology and human ingenuity can solve any and all problems. Actually, I like to believe that they can, but *only* if directed at the real problems.

Every day there are more people adding suffocating pressure on biological systems and species. With each passing day the genetic basis of our agriculture becomes narrower. With each passing day fewer species inhabit the planet. And the planet's fundamental (biological) capacity to support human societies diminishes. We rush, fecklessly, toward a genetic anorexia. The pages that follow demonstrate the need to slow and eventually check this continuing impoverishment of our biological resources. The Earth should not be the poorer for our existence.

Dr. Thomas E. Lovejoy
World Wildlife Fund

Preface

In his preface to Christopher Stone's timely book *Should Trees Have Standing?,* Garrett Hardin wrote:

> From our ancestors we inherit three sorts of things: material objects, genes, and ideas. Of these three the first is least important, for "a fool and his money are soon parted." The other two inheritances leave more lasting traces.

In this book, I have attempted to amass specific information about how we use our most valuable intergenerational resources—genes and ideas—to sustain the socioeconomic systems that produce the material objects we use, in turn, to sustain and enrich human life. I have also endeavored to pinpoint the major sociocultural ideas—our attitudes and conceptualizations—that influence our efforts and abilities to conserve our global genetic heritage and to deal with the impending genetic crisis.

Because we cannot immediately see and touch genetic materials and because their biological sources and economic uses are often obscure to us, it is difficult to discern the essential role they play in sustaining our lives and societies. When I began intensive study of this subject in 1975, I was already aware of the dependence of much of our economic productivity on the survival and continuing maintenance of natural environments and traditional agro-ecosystems, their wild or relatively unimproved biota, and the genes we obtain from these natural resources. However, as the years have passed, I have been surprised to discover, especially within my homeland—the United States—just how much our economic systems are actually sustained by these living resources. Moreover, the information I have garnered for this book is only a beginning—just the tip of an iceberg, or perhaps I should say a glacier! Furthermore, although I was aware of the accelerated pace of species extinctions and genetic erosion of recent times when I initiated my work on this topic, I did not realize just how rapidly and extensively we are losing our accumulated genetic wealth. Whereas I had originally thought that massive genetic losses and their socioeconomic consequences—a worsening condition for national economies and the global economy as a whole—would not become a serious problem for at least a century or more, I can no longer be so optimistic.

I now believe that without an immediate and dramatic change in our attitudes about conservation of our genetic heritage by the turn of the century or shortly thereafter, nothing will forestall significant reductions in economic productivity due to the progressive deterioration of essential biotic-support systems. Thus, the fate and survival of nations, and possibly the welfare of the entire human species, will probably be decided by the present generation within the coming decades: if the energy crisis does not destroy the backbone of modern industrialized economies, the impending genetic crisis eventually will. The symptoms of such a crisis are already upon us: the massive losses of crop and livestock gene resources, accelerating rates of species extinctions, and the progressive conversion of valuable natural genetic reservoirs to more short-term economic uses. Unfortunately, if we cannot effect national and international conservation of these essential natural resources, the world will be in the midst of a major genetic crisis near the turn of the century.

The developed and the developing nations have acquired very disparate ideas regarding the location and use of genetic resources. The orientation and focus of both basic and applied research at the national level reflect these differences. In the United States and other technologically advanced nations, the direction of scientific research (and the nature of industrial activities) is usually well developed with respect to achieving novel applications of biotic resources. But we lack much of the diversified, basic scientific orientation and transdisciplinary research within science and industry needed to fuel these technological processes. Contrastingly, in the less technologically advanced nations, the orientation of scientific research is relatively well developed with respect to economic biology and ethnobiology—two subdisciplines of biology which have greatly facilitated the discovery and use of our genetic heritage. Yet, they lack much of the scientific expertise and technological know-how needed to rapidly develop and use genetic resources for socioeconomic and industrial purposes. Both approaches are necessary. Perhaps this, at least in part, explains the continual flow of agricultural, medicinal, and industrial genetic resources (along with ideas about how to use them) from the developing to the developed nations, and the simultaneous reverse flow of technological and scientific ideas from developed to developing nations about how to obtain a better technological capacity to improve and more efficiently utilize these natural resources to serve the needs of more people.

Aside from the differences in national needs, such disparate national attitudes toward the location and exploitation of useful genetic resources can be partially attributed to differences in the respective stage of industrialization and extent of economic organization of developed vs. developing nations. As a consequence of the industrialization process and many generations of movement from rural to urban-industrial areas, most of the people in technologically advanced nations have become very disassociated from the land and land-based production processes. Technological gadgetry and artificially produced goods have become socially accepted and even revered as signs of socioeconomic "progress," while such items as wild foods, or medicinal and industrial plants and animals, and even hand-raised garden crops have become associated with "primitive conditions" or "backwardness." Some people have taken this line of reasoning to the point of absurdity, asserting that those who suggest that we go "back to nature" to search for new economic resources are necessarily asking us all to go back to the old days when times were harder and we lacked many of our familiar modern conveniences. Actually however, nothing could be further from the truth. Overemphasis of technological progress with concomitant failure to more fully develop our biotic production potential and to conserve our genetic heritage for future socioeconomic needs now threatens to

propel us rapidly back to harder times. The reasons for this can be gleaned from the various case studies provided in this book: a great proportion of our economic productivity is directly or indirectly tied to the value of wild and relatively unimproved gene resources, and the unexplored economic potential of obscure or poorly known biota is immense. Most of us who live in modern, industrialized societies have been ignoring these realities. And although ignorance is bliss at times, it may eventually precipitate an economic or political disaster of major proportions. We not only have much scientific and technological knowledge which could be used to aid the peoples of lesser developed nations, but we also stand to gain much in return.

Finally, considering our slowly evolving ideas about how to conserve our accumulated genetic wealth, the recent emphasis on the need for international diplomacy and cooperation to the mutual advantage of all nations is the most important of all. Conservation and improved use of living resources should be accomplished internationally for all peoples as well as for future generations because, to give a few reasons:

- Conservation or management of many species transcends regional or national boundaries.
- Crops (or livestock) that originated in one country are likely to be more productive in a suitable foreign environment.
- Most modern agro-ecosystems are based on introduced domesticates and genetic materials, and thus they ultimately depend on other nations for needed biotic resources.
- The pharmaceuticals and industrial raw materials harbored within the biota conserved by one nation may be used for the benefit of mankind worldwide.

Despite these practical reasons for international conservation of gene resources and moral and philosophical arguments, global conservation remains a disorganized and often competitive or nationally self-serving endeavor. Most countries or national organizations are concerned with obtaining and "preserving" useful sources of genes to promote the future economic welfare of their own nation. Considering the great value of living resources to all socioeconomic systems—whether private enterprise or socially planned, modern or pre-modern—it is no wonder that this tendency exists.

Nevertheless a nation-centered approach to conservation carries with it many unfortunate consequences which act to inhibit conservation on a global scale. For example, in the past a fairly common method for building national *ex situ* reservoirs of genetic materials has been the practice of exploiting the resources available within *in situ* genetic reservoirs (national parks, wildlife reserves, etc.) of other countries. There has been little interest in the idea of providing financial or technical aid to these countries to facilitate conservation of these natural reservoirs *per se*. Some have even denounced the idea of national contributions to support international conservation programs because they seem "impractical;" i.e., it is difficult to ensure future access to these areas or the implementation of effective conservation policies in return for present aid expended. One of the consequences of this lack of interest and support is the increasing scarcity of available reservoirs of genetic diversity. A common experience of plant and animal collectors over the last few decades has been that of returning empty-handed from favored or previously valuable collecting sites within crop centers of genetic diversity. Similar trends are now being observed with respect to resources harbored within the world's diminishing tropical forests. The attitudes of consumers within industrialized nations also militate against *in situ* conservation efforts in foreign countries. As an example, Americans and Europeans com-

monly pay $1,000 or more for a rare bird or other exotic pet from a tropical forest, thus contributing to the depletion of valuable wildlife populations and the alteration of their tropical habitats. Yet how many of these wildlife consumers in the affluent nations would be willing to pay 5 percent or even 1 percent of the purchase price as a conservation tax to support efforts to conserve the living resources they are helping to destroy?

Since a great proportion of the useful biotic resources of the earth have yet to be discovered or genetically improved, and since most wild species cannot be easily or effectively maintained artificially outside their native habitats, a continuation of such nationally oriented conservation and use strategies will be self-defeating over the long run. We must begin to look beyond our own patriotic and individual needs or desires, so that we can seek global conservation solutions that will enhance the quality-of-life for mankind as a whole. We have much to gain by cooperating with each other and with other nations in order to conserve our genetic heritage, and too much to lose if we fail.

Acknowledgments

There are a great many people without whose collaboration and assistance the execution and completion of this book would have been much more difficult. I would especially like to thank the following persons for their help in developing portions of specific case studies: Dr. A. Jack Oakes, Crop Germplasm Resources Laboratory, USDA-ARS Federal Research Center, Beltsville, MD (erosion of crop germplasm resources; leucaena; cinchona); Dr. Leland W. Briggle, National Program Staff, USDA-ARS Federal Research Center, Beltsville, MD and Mr. Jim Naive, USDA Commodity Economics Division, Washington, DC (value of crown rust-resistant oats production); Dr. John L. Creech (genetic erosion; coffee; cinchona) and Dr. Frank S. Santamour, Jr. (breeding and conservation of ornamental/urban trees) of the U.S. National Arboretum, Washington, DC; Dr. Stanley L. Krugman, Timber Management Research Division, USDA Forest Service, Washington, DC (economics of timber tree improvement programs); Dr. Ernest P. Imle, International Programs Division, USDA-ARS, Hyattsville, MD (*Hevea* rubber; coffee and coffee rust; rust-resistant oats); Dr. Robert E. Perdue, Jr., Plant Taxonomy Laboratory, and Dr. James A. Duke and Dr. Arthur S. Barclay, Economic Botany Laboratory, USDA-ARS Federal Research Center, Beltsville, MD (NCI anticancer plant screening program); Drs. Matthew Suffness and John Douros, Natural Products Branch of the Plant and Animal Screening Program, National Cancer Institute, Bethesda, MD (NCI anticancer compounds); Dr. Bruce MacBryde, Office of Endangered Species, U.S. Fish and Wildlife Service (USDI), Washington, DC; and Mr. David Mack, TRAFFIC (U.S.A.), Washington, DC (wildlife trade and endangered biota).

Many other people have also provided me with important information; I have benefited from discussions or correspondence with: Dr. Garrison H. Wilkes, Biology Department, University of Massachusetts, Boston (maize and teosinte); Dr. Daniel W. Gade, Department of Geography, University of Vermont, Burlington,; Dr. Stephen B. Brush, Anthropology Program, National Science Foundation, Washington, DC,; and Dr. Efraim Hernández X., Colegio de Postgraduados, Chapingo, Mexico (role of human cultural diversity in enchancing crop genetic diversity); Dr. Desmond D. Dolan, USDA-ARS New York State Agricultural Experiment Station, Geneva (disease resistance value of wild tomato species); Dr. T.T. Chang, International Rice Research Institute, Manila, Philippines (value of primitive and wild

rices); Dr. Grover Sowell, USDA-ARS Southern Regional Plant Introduction Station, Experiment, GA (value of peanut leafspot-resistant gene resources); Dr. Pierre G. Sylvain, Centro Agronomico Tropical de Investigacion y Enseñanza, Turrialba, Costa Rica (breeding of rust-resistant coffee cultivars); Dr. S.M. Dietz, USDA-ARS Western Region, Pullman, WA (new crops—value of U.S. soybean introduction); Dr. E.A. Oelke, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul (domestication of wild-rice); Dr. W.H.P. Emery, Biology Department, Southwest Texas State University, San Marcos, and Mr. Harold E. Beaty, Temple, TX (Texas wild-rice); Dr. Norman R. Farnsworth, Department of Pharmacognosy and Pharmacology, University of Illinois at the Medical Center, Chicago (economic value of natural drug products); Dr. Alfred Weinheimer, College of Pharmacy, University of Houston, Houston, TX (anticancer compounds from marine organisms); Dr. T.R. Sweeney, Department of the Army, Walter Reed Army Hospital, Institute of Research, Washington, DC (malaria chemotherapy and U.S. troops); Dr. Nancy Muckenhirn, National Academy of Sciences, Washington, DC (biomedical value of nonhuman primates); Dr. Peter H. Raven, Missouri Botanical Garden, St. Louis (tropical deforestation); Dr. Noel Vietmeyer, National Academy of Sciences, Washington, DC (underutilized leguminous trees); Dr. James L. Brewbaker, College of Tropical Agriculture, University of Hawaii at Manoa, Honolulu (genetic improvement of leucaena); Dr. Constantine Alexopaulos, University of Texas, Austin (rubber/economic botany); Dr. Russell A. Buchanan and colleagues, USDA Northern Regional Research Center, Peoria, IL, and Dr. Melvin Calvin, Laboratory of Chemical Biodynamics, University of California, Berkeley (rubber- and oil-bearing plants); Mr. William P. Miller, Bureau of Indian Affairs, U.S. Department of the Interior, Washington, DC, and Drs. William G. McGinnies and Leslie Rawles, Office of Arid Lands Studies, University of Arizona, Tucson (guayule, jojoba, arid lands plant resources); Mr. Arthur S. Kavaler, Schnell Publishing Company, New York, NY (sperm oil economic data); Dr. Tom Lovejoy, World Wildlife Fund, Washington, DC (accelerating rates of species extinction); Dr. John A. Burton, IUCN/SSC TRAFFIC Group, Zoological Gardens, London, England, Dr. Rene Honegger, Zurich Zoo, Switzerland, Dr. F. Wayne King, New York Zoological Society, New York, Dr. Howard Campbell, National Fish and Wildlife Laboratories, Gainesville, FL, and Lt. Col. Brantley Goodson, Florida Game and Fresh Water Fish Commission, Tallahassee (value of illegally traded endangered wildlife and wildlife products); Drs. Paul Opler, Kenneth Dodd, John Fay, and Jay Shepherd, Office of Endangered Species, U.S. Fish and Wildlife Service (USDI), Washington, DC (U.S. endangered species); and Dr. Robert M. Pyle, The Nature Conservancy, Northwest Office, Portland, OR (endangered butterfly species).

I would also like to extend thanks to the U.S. Department of Agriculture officials and scientists who helped acquaint me with the plant germplasm conservation facilities, equipment, and activities in the United States, especially Dr. George A. White, Crop Germplasm Resources Laboratory, USDA-ARS Federal Research Center, Beltsville, MD; Dr. Louis N. Bass, U.S. National Seed Storage Laboratory, Fort Collins, CO; Dr. W.R. Langford, Southern Region Regional Plant Introduction Station, Experiment, GA; and Drs. Paul K. Soderholm and Robert Knight, USDA-ARS Subtropical Horticulture Research Unit, Miami, FL. In addition, I would like to thank Dr. Norman Myers, Consultant in Environment and Development, Nairobi, Kenya; Dr. Robert Jenkins, The Nature Conservancy, Arlington, VA; Ms. Judy Bevis, Cultural Survival, Inc., Cambridge, MA; Ms. Barbara Bentley,

Survival International, London; Mr. Earl Baysinger, Survival Service Commission, International Union for the Conservation of Nature and Natural Resources; Dr. Nicole Duplaix, TRAFFIC (U.S.A.), Washington, DC; Drs. Norman Borlaug and R. Glenn Anderson, Centro Internacional de Mejoramiento de Maíz y Trigo, Mexico, DF; and Dr. David Kafton, National Council for Gene Resources, Berkeley, CA.

Photographs and illustrations were kindly supplied by: Dr. Noel Vietmeyer of the National Academy of Sciences (leucaena; manatee); Dr. Garrison Wilkes of the University of Massachusetts with permission of *Economic Botany* (teosinte and maize); Dr. W.H.P. Emery of Southwest Texas State University (Texas wild-rice); Dr. Robert E. Perdue, Jr. of the USDA-ARS Federal Research Center, Beltsville, MD (illustrations of plants yielding anticancer compounds); and the National Archives Audiovisual-Still Picture Library, the U.S. Department of the Interior Photo Library, the U.S. Department of Agriculture Photography Division, and the USDA Forest Service Audiovisual Library.

Useful comments and constructive criticism on the various drafts of portions of the book were provided by: Drs. Lawrence R. Lawlor, Lawrence E. Gilbert, Richard Richardson, W. Frank Blair, and Alcinda Lewis of the Department of Zoology, Beryl B. Simpson and Ms. Janis B. Alcorn of the Department of Botany, and Dr. Paul Szaniszlo of the Department of Microbiology, University of Texas, Austin; Dr. Stanley Krugman, Timber Management Research, USDA Forest Service; Dr. A. Jack Oakes, USDA Crop Germplasm Resources Laboratory, Beltsville, MD; Dr. Garrison Wilkes, Biology Department, University of Massachusetts, Boston; Drs. Bruce MacBryde and Ray Stanton, Office of Endangered Species, and Mr. Richard L. Jachowski, Office of the Scientific Authority, U.S. Fish and Wildlife Service (USDI), Washington, DC; Dr. Linda McMahan, TRAFFIC (U.S.A.), Washington, D.C.; and Dr. Gardner M. Brown, Jr., Department of Economics, University of Washington, Seattle. I would also like to thank Mr. Vernon C. Gilbert, Jr. of the International Science and Technology Institute, Inc., Washington, DC; Dr. Theodore W. Sudia of the National Park Service, U.S. Department of the Interior, Washington, DC; and Dr. Rezneat M. Darnell, Texas A & M University, for their advice and encouragement, especially during the early stages of the project.

I would like to acknowledge the research support of the National Park Service, U.S. Department of the Interior (Contract No. CX0001-7-0017) for completion of the draft report on which this book is based. I would also like to extend appreciation to my library and research assistants and the Texas System of Natural Laboratories, Inc. for their contributions to my research and completion of the draft report. Moreover, I am especially grateful to the following people for their assistance in the development of certain case studies: Ms. Leah Miller (background work on endangered species); Mr. Jim DiGiulio (biological control examples); Dr. Elizabeth Evans (speciation vs. extinction rates); and Ms. Janis Alcorn and Dr. Alcinda Lewis (plant breeding and economic botany literature survey). I would also like to extend my thanks to the people of the Division of Biological Sciences, the University of Texas, and to my thesis advisors at the Pennsylvania State University—for without their willing support and advice, I might not have initiated my work in this subject area. And finally, I am grateful for the moral support and understanding of my family and friends who endured my many moods and long nights at the typewriter for the duration of this research project.

M.L.O.
July 1981

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The Value of Conserving
GENETIC RESOURCES

BY
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1

Gene Resource Conservation: A Socioeconomic Necessity

Genetic resources and the habitats that sustain them may well come to be recognized as our most important economic and political assets. These resources are dependent on the great diversity of genetic materials contained both within and among populations of living organisms. Although unseen, but for their results, genes are vital natural resources. Without them and their carriers' essential habitats, no human civilization could long endure, and modern industrialized society could not exist as we know it today.

In this technological age, our economic prosperity and our everyday existence seem unrelated to genetic resources and the earth's remaining natural areas and traditional farming systems. We tend to view conservation of these resources and the environments that harbor them as a luxury—something we can think about if we have any time or funds left over after we take care of such seemingly more practical concerns as employment, energy, defense, commerce, health care, housing, and transportation. Yet we fail to recognize that genes as natural resources contribute significantly to each of these socioeconomic concerns. In fact, genetic resources and their requisite environments contribute many billions of dollars worth of raw materials or unprocessed products to the U.S. economy each year. Without these natural resources, many basic commodities and luxury goods, and therefore many jobs, would not exist; furthermore, numerous other commodities would be available only at much greater cost.

Consider, for example, the United States' recent success in sending the Columbia Space Shuttle into orbit. As millions of Americans watched Columbia's breathtaking landing, very few realized that 95-98 percent of the rubber in the tires was natural rather than synthetic rubber. Although natural rubber is obtained from a semi-domesticated tropical tree, the wild relatives of this industrial crop contributed essential genetic materials during the course of its domestication, and they still play a

major role in supporting the natural rubber industry. Timber is another industrial raw material obtained from trees; it must be stockpiled for national defense purposes. Some tropical hardwoods, although now scarce or very expensive, are especially valuable for sustaining U.S. naval operations. Virtually all timber is obtained from wild trees, because even though some wood-producing species are grown on plantations, not one of these cultivated timber species is truly domesticated as are all of our major crop plants.

Similarly, much of our agricultural productivity depends on the conservation of wild plants and animals and the genetic materials we obtain from them. Even though most of our food is produced by domesticated species today, all crop and livestock species ultimately trace their ancestry to wild biota. Moreover, nearly all modern crop varieties and some highly productive livestock strains contain genetic material recently incorporated from related wild or weedy species, or from more primitive genetic stocks still used and maintained by traditional agricultural peoples. Likewise, both wild and cultivated biota are important contributors to the pharmaceutical and health services sectors. Even though most people in industrialized nations believe that nearly all drugs are chemically synthesized, actually at least two-fifths of all modern U.S. pharmaceuticals contain one or more naturally derived ingredients.

In short, genetic resources from wild species and primitive forms of domesticated plants and animals provide the biotic raw materials that underpin every major type of economic endeavor at its most fundamental level. By ensuring the well-being of other life forms, we ensure our own well-being and survival. Many of us would save endangered wildlife or crop and livestock gene resources for historical interest or love of wildlife or esthetics. However, their most important value is their hidden potential for enhancing the quality of life for present and future generations. It is upon this that our quality of life—and life itself—depends. Thus, an endangered Mexican teosinte species—one of the closest wild relatives of maize or corn—may provide us with the genetic materials needed to convert corn from an annual to a perennial crop, making temperate gasohol production more feasible. The endangered and protected species *Zizania texana* (Texas wild-rice) may yield disease resistance genes or other economically useful genes for the domestication and improvement of wild-rice, its northern relative which promises to be the world's newest grain crop. The endangered Guatemalan fir could, if it survives, be developed as a firewood-producing species for now treeless, mountainous tropical areas. And a rare African shrub recently contributed to our ongoing efforts to discover and develop new anti-cancer drugs. Moreover, a great number of species that have become endangered as a result of economic exploitation could be used for other socioeconomic purposes, if not for their present endangered status. Thus, the many species of endangered manatees, valued for their edible flesh and oil, might otherwise be used today for controlling noxious, exotic waterweeds that clog industrial waterways or cover aquatic recreational areas. Many tropical meat-producing animals could be domesticated as stock for game ranches, if they were not already threatened as a result of such activities as international trade in hides, horns, or bushmeat, or sport hunting for trophies.

And what, we may ask, is the potential economic value of the snail darter or the Furbish lousewort? As we continue our scientific endeavors and increase our applications for naturally derived products, an ever-increasing number of previously "useless" species will assume economic importance. We will come to understand

that there is really no such thing as a useless plant or animal; rather there are organisms for which we have yet to discover a use. Scarcely a century ago, natural rubber was virtually unknown to more advanced civilizations, yet today it is an essential industrial raw material, the value of which increases each year as the price of petroleum-based synthetic rubbers continues to rise. Similarly, before 1900 virtually no use was made of crop genetic resources by advanced societies; although selection for desirable traits was being practiced, intensive plant breeding efforts using foreign gene resources began only in the following decades. Yet today our high-yielding modern crop varieties could not long endure in our modern agro-ecosystems without a constant influx of disease resistance genes from traditional agro-ecosystems and natural areas within foreign countries. There are numerous examples of crop genetic resources that were harvested from Europe, Africa, Asia, and Latin America during the 1930's and 1940's, yet they were not discovered to be useful to plant breeding until the 1960's and 1970's.

Conservation, most simply stated, is the wise use of natural resources. It does not imply that everything should remain in a pristine state, or that every species or every form of genetic resource must be preserved in perpetuity. However, it does mean that renewable resources, especially genetic resources, need to be carefully managed so that they are not directly overexploited or the processes and habitats necessary for their replenishment are not destroyed. Genetic resources are among the very few economic resources that are potentially inexhaustible. As long as we conserve sufficient quantities of representative natural areas and high-quality habitats—both natural and man-modified—and so long as we exploit them in a way that will allow replenishment, genetic resources can continue to furnish us with their products indefinitely and provide us with a sound basis for future technological progress. Unfortunately, habitat conservation decisions, if made at all, are most often haphazard and made for purely esthetic or recreational reasons, or they are considered only after all of the prime habitats have been thoroughly developed. Moreover, many economically valuable species, some of which support multi-million dollar extraction industries, have been continually exploited to the point of commercial extinction and are now so depleted that they are probably doomed to biological extinction as well.

Ironically most of the concern expressed today about the increasing scarcity of natural resources centers on the depletion of nonrenewable resources, such as petroleum, natural gas, metals, and minerals. Yet nearly all of the well known and established cases of total resource exhaustion are biological—i.e., once renewable—resources. As available supplies of nonrenewable resources become depleted, technological improvements are devised which allow new and better opportunities for extracting or using lower-quality resource stocks. In contrast, once we have depleted a species to the verge of extinction, technology can do very little to save it. Most species require relatively large numbers of individuals to survive and continue to adapt to changing environmental conditions. Aside from the issue of harvesting far too many individuals, some of our most common harvesting practices involve the extraction of the economically best or most biologically fit specimens, and therefore remove much of the prime genetic stock. Technology cannot recreate a lost genome or gene complex or bring back an extinct species, nor can it halt the extinction of a species so depleted in number that it is biologically doomed. For these reasons, more attention should be paid to the ever-increasing number of renewable biological re-

sources that are being shifted to nonrenewable resource status or are being lost entirely as a result of extinction.

What to Conserve

The term genetic resources, or gene resources, refers to the economic or societal value of the genetic materials contained within or among species. For the most part genetic resources are natural resources—economic raw materials that are supplied to us as a result of natural processes. In contrast, man-made resources are ultimately derived from natural resources, but they are usually altered significantly or manipulated by human ingenuity to take on shapes or forms very different from those found in nature. A few important gene resources, particularly those of domesticated species, are the combined result of both natural and man-directed processes. Genetic resources are also renewable natural resources. In other words, they are inexhaustible *unless* the physical, geochemical, or biological basis for their continuing formation is destroyed. In contrast, nonrenewable resources provide a fixed or finite supply of products, and they are therefore considered exhaustible over the long run.

Considering the great number of renewable resources that have become exhausted through overuse (and the few examples of nonrenewable resources so exhausted), it is important to point out that genetic resources are only potentially renewable. They can be viewed as renewable resources only so long as their populations (stocks of breeding individuals), and therefore the genetic materials they contain, are properly managed and conserved for long-term use. A potentially renewable genetic resource can be all too easily rendered nonrenewable through extinction or extensive reductions in population size. The shift of a wildlife resource from a renewable to a nonrenewable resource category can occur in two major ways:

- Directly, through over-exploitation of the species or its distinct populations; or
- Indirectly, through destruction or extensive alteration of the specific habitat(s) on which the resource populations depend for their survival, including disruption of ecological relationships with other species, e.g., pollinators, seed dispersers, which help to maintain its populations.

The latter point underscores the importance of the environment and of other species within the wildlife community. No gene resource population can exist without a habitat, be it a cold storage or "gene bank" facility, an arboretum or zoo, a traditional agro-ecosystem, or a natural ecosystem.

The first part of the term—genetic—indicates that the resources in question are dependent on the structure and function of the genetic information contained within living organisms. The structural and functional unit of inheritance, and the unit in which genetic information is packaged, is the gene. For each living organism, the observable (phenotypic) traits are determined primarily by its underlying genetic constitution and partly by environmental influences; it is the genes, however, that determine the capacity or limits for the expression of observable characteristics. Moreover, only alternative forms of genes—called alleles—can be passed from one generation to the next through the process of reproduction. Thus, genes are units that transcend generations, and it is the intergenerational nature of genetic material

coupled with the environment and the constant and free energy of sunlight that ultimately allows all biological resources to be potentially renewable.

New alleles or forms of genetic diversity are accumulated by mutations—structural changes in the genetic information that constitutes a gene. Mutations can be induced naturally, e.g., by ultraviolet radiation, or artificially, e.g., by human-produced chemical mutagens. As the ultimate source of all genetic diversity, mutations are the basis for evolutionary change in populations. Evolution at its most basic level is merely a change in the frequency or proportion of various alleles of a gene within a population over time. Once a mutation has occurred and has become successfully established within a population, other evolutionary forces—migration, selection (either natural or artificial), or genetic drift—may come into play to alter the proportions of the different alleles which exist within the gene pool of a population.

A gene pool is the sum total of all of the genetic information within a population of interbreeding or reproducing individuals. On the other hand, germplasm is the genetic material that constitutes the physical basis of the heritable portions of one organism's traits or characteristics. Both the germplasm of specific individuals and the gene pools of an entire breeding unit or species can be used as genetic resources. However, since germplasm resources are ultimately extracted from gene pools, gene pool resources (and therefore populations or species) possess far more potentially useful genetic variation than the germplasm resources or individual specimens derived from them. When we need a new economic species, scientists usually search among different gene pools, i.e., distinct populations or species, in order to locate those which exhibit the greatest potential for supplying the desired product. The goal is thus to discover a new resource by capitalizing on the genetic diversity that exists among different groups of organisms; this is often referred to as using interspecific or interpopulational genetic diversity. For example, when researchers seek new natural sources of anticancer compounds, they would be wasting their time to inspect new populations of the same species that has already provided an anticancer drug, because the germplasm resources they would extract from these sources would most probably yield the same or very similar chemical compounds. Instead, as a rule, they would focus their search on related, but different species, on geographically, very distant—and therefore genetically distinct—populations, or on totally unrelated species.

On the other hand, once a particular species or population is widely cultivated or has been domesticated for production of a particular economic product, there is usually a concerted effort to exploit the germplasm resources derived from its various gene pools. In this instance, the goal is to genetically improve or alter an extant resource by tapping the heritable differences found within a species (intraspecific) or its populations (intrapopulational). As an example, suppose a plant collector is sent to a foreign country to locate drought-resistant germplasm so that a crop species can be genetically improved for cultivation in low rainfall areas. The collector will tend to look for and collect germplasm resources from the crop's wild or cultivated populations that border on or extend into semi-arid or very dry habitats. Generally speaking, then, genetic variation observed among gene pools is more instrumental in locating new sources of economic species or products, whereas differences among the germplasm resources represented by different individuals within a gene pool tend to be more useful for the genetic improvement of preferred

economic species or populations.

In summary, economically valuable gene resources are obtained from individuals of wild, weedy, or domesticated species; in some instances, gene resources have also been obtained through artificial induction of single gene mutations. The major types of genetic resources currently used for socioeconomic purposes are discussed briefly in the Appendix, along with information about the most common and appropriate conservation strategies recommended for each.

How to Conserve

The two basic methods for conserving genetic diversity are the *in situ* and *ex situ* conservation strategies. *In situ* conservation (natural ecosystem or habitat conservation) entails the management or conservation of genetic resources within their natural or original habitat. In contrast, *ex situ* conservation methods involve removing individuals (or their reproductive parts) for management or preservation in an alien environment. *Ex situ* storage environments include "gene banks" or cold storage facilities and other methods of cryobiological preservation of plant and animal materials, "mass reservoirs," and collections of individual resource stocks maintained in zoos, arboreta, aquaria, plant or animal introduction and propagation facilities, and, for microorganisms, type culture collections.

The Importance of Conserving Natural Ecosystems

In situ conservation is generally preferred for aquatic species and all wild terrestrial species, particularly obscure or taxonomically unknown, and endangered or threatened species. Most of these cannot be conserved effectively by available *ex situ* methods. Although it is typically a simple task to remove some wild germplasm resources (individuals) from their native environments and place them in appropriate *ex situ* environments, it is impractical, if not impossible, to preserve the entire gene pool of a population, much less an entire species, by *ex situ* means. By carefully and systematically sampling the germplasm resources within a gene pool of a wild species, a significant proportion of the genetic diversity available can be adequately sampled for *ex situ* conservation. However, it is unlikely that the germplasm sample thus obtained will contain all of the qualitatively useful genetic information that the gene pool has to offer. Moreover, once the extracted resources have been established elsewhere to found a new population, some reductions in genetic diversity will be inevitable due to selection in the new environment. For domesticated or cultivated biota both *in situ* and *ex situ* conservation methods are needed. *Ex situ* conserved resources are necessary and important adjuncts for any genetic improvement program. However, *ex situ* strategies are not a panacea for conservation of the genetic resources which form the biotic basis of a number of important economic production processes, primarily because *in situ* reservoirs of genetic materials are ultimately needed to provide biotic sources of *ex situ* resources.

Moreover, *in situ* conservation is often preferable to *ex situ* strategies for a number of other important reasons. In the first place, seeds or other reproductive parts of many plant species cannot be stored in gene banks or by any currently available cryobiological preservation techniques. Examples include many tropical crops (especially fruit- and nut-producing species); many timber and medicinal species; orchids and many other ornamental plants; and *Hevea* rubber. Additionally, although semen samples of many animal species can be successfully stored cryogenically, techniques have not yet been developed that enable the safe and effective storage of animal eggs. Moreover, maintenance of these "recalcitrant" resources via mass reservoirs or other *ex situ* means is frequently cost-prohibitive; it is often cheaper and more desirable to preserve such genetic stocks *in situ*. Also, cryobiological preservation does not provide an adequate mechanism for the conservation of endangered or threatened species. One cannot conserve the germplasm represented by an entire species by preserving one or a few individual organisms in a gene bank, even if one can store individuals or reproductive parts of that species cryogenically. If a plant or animal species is endangered or has been reduced to a few hundred or thousand individuals, much of its former genetic diversity will have already been lost. Such species may well be on an irrevocable path to extinction, and *ex situ* preservation of some of the few remaining individuals will probably be a futile effort which will only serve to further deplete its natural population(s). Furthermore, many taxa require other species or specific environmental conditions in order to survive; thus, they cannot be easily or effectively maintained in arboreta, zoos, aquaria, or other *ex situ* facilities. Finally, to "save" an endangered or threatened species, requires a suitable natural habitat into which the species can ultimately be "reintroduced," for the environmental selection pressures within *ex situ* facilities are very different from those to which the species has been exposed during its evolutionary history. A species maintained entirely by *ex situ* means for many generations may no longer be capable of surviving in a natural environment without the assistance of man. All of these considerations point to the importance of conserving wild or endangered species by *in situ* means, i.e., by conserving their natural habitats.

Second, economically important genetic traits and specific adaptations exhibited by resource populations are acquired through dynamic evolutionary processes within natural environments. Consider, for example, a trait such as disease resistance. Since cultivated populations of modern cultivars are not subjected to the natural selection pressures of their pests and diseases year after year, they do not have the opportunity to naturally develop their own genetic resistance traits. Therefore, advanced crop cultivars used in modern monocultural agro-ecosystems, such as those in the United States, only rarely, *if ever,* acquire disease resistance traits naturally. Crop disease and pest species are generally more flexible genetically than are the higher organisms they attack. Monocultures—large acreages planted in a single crop variety—facilitate epidemics of diseases and pests, because the modern varieties we plant over extensive areas are strikingly genetically uniform. They do not possess the genetic diversity needed within their populations to withstand the ravages of a new virulent form of a coevolved disease pathogen or insect pest. On the other hand, populations of wild crop relatives are typically genetically diverse; they stand a much better chance that some individuals will be genetically capable of tolerating or resisting such attacks, thus surviving to reproduce and perpetuate the population.

Similarly, traditional farmers can choose seeds from the most healthy, disease-free plants of their primitive cultivars, saving them for next year's crop and consuming the others. Even if selection is not consciously practiced, the crops are maintained more or less in a natural state since their populations remain in constant contact with the selective pressures of their common diseases and pests. Only the offspring (seeds) from plants that have been able to survive the attacks of such predators or parasites can be used to establish the next year's crop. In contrast, when our modern crop varieties eventually succumb to the ravages of a new mutant form of pathogen or pest, plant breeders turn to stored or conserved seed stocks (or other reproductive materials) of primitive cultivars, wild or weedy species, or sometimes to obsolete, improved varieties, to find the needed resistance genes. In other words, genetic resistance traits acquired naturally by wild, weedy, or primitive stocks, or genes from these species which have been incorporated within obsolete cultivars, are used to supply the necessary resistant germplasm that keeps our modern crop varieties economically productive.

So, if we obtain needed resistance genes from the seed stocks we have preserved in gene banks, why not just store them there and forget about preserving resource populations in the natural or man-modified environment? There are two major problems with reliance on such a strategy. One is that for some of our major crops, all of the available stored resources known to possess genetic resistance to certain pest organisms have already been exhausted. To obtain new stocks, we must go back to the remaining *in situ* genetic reservoirs, or rely on mutation breeding techniques. More important, if one stores seeds now for future use, there is no guarantee that 10, 20, or 30 years from now the stored resources will possess effective resistance against a constantly changing (mutating) pest population. In fact, considering the great genetic plasticity possessed by most pathogen and insect populations, the opposite would be expected. In short, in order for a resource population to acquire and maintain genetic resistance to pests, the population must continue to be influenced by the selective pressures of its pest population(s). Although this may be simulated under laboratory conditions, it can be accomplished more effectively by retaining natural populations of wild relatives of crop plants or agricultural populations of primitive cultivars. Because they are removed from their man-modified or natural environments, cold-stored seed stocks are incapable of responding to counteradaptive mutations for virulence in the pest populations that commonly attack our crops in the field or their wild relatives in nature.

Finally, there are sampling problems and actual physical limitations involved in the use of *ex situ* conservation methods, particularly cold storage. Moreover, when gene resources are maintained in gene banks some seeds or pollen may survive, while other individuals or stocks which are susceptible to the hazards of storage may not. Diversity-reducing selection processes can also occur whenever seeds or pollen are removed from cold storage for purposes of rejuvenation and seed increase; such cycles must occur periodically, the periodicity being determined by storage conditions and the particular crop in question. After only two or three storage and rejuvenation cycles, many original entries will retain little genetic resemblance to their original parental stocks collected from nature. In addition to such genetic drawbacks, duplications and gaps exist in *ex situ* collections. Furthermore technical, political, and financial problems sometimes occur when maintaining gene resources by cold storage or other *ex situ* means.

Why Conserve Natural Genetic Diversity?

Genetic variation can be induced through the use of mutation breeding techniques and employed in the crop improvement process. Yet even though both human-induced and natural genetic variation can be useful to mankind, artificially induced genetic alterations cannot supplant our need for natural sources of genetic diversity. In certain circumstances, it is necessary to rely on artificial induction of mutations, and two major reasons have been advanced for the need to master the techniques of mutation breeding. First, for some crops, particularly self-pollinating, and highly inbred or vegetatively propagated ones, most of the *ex situ* stored natural sources of genetic diversity have already been utilized or it has proved difficult to transfer useful genes from wild or primitive germplasm resources using conventional breeding techniques. In these cases, it is often preferable to induce mutations in advanced or modern crop cultivars. Second, extensive losses of genetic variability have already occurred for some crop species. If nearly all of our natural sources of useful genetic attributes have been lost, the only recourse may be artificial induction of mutations.

However, for a number of reasons we cannot rely entirely on induction of mutations in place of natural sources of genetic diversity. Mutation breeding requires the irradiation or chemical treatment of massive quantities of seeds (or pollen); since most of the mutations produced are harmful, most of the treated seeds will not be able to develop into viable plants. Practical techniques for removing genes that determine an economic trait from inviable plants have not yet been developed. Once a collection of plants has been obtained from the treated stocks; the next step is to design an effective screen—a mechanism for selecting among the survivors to find a specimen which might have acquired a biologically harmless, but economically useful change in its genetic constitution. For many traits, such as disease resistance, efficient and cost-effective screens already exist; yet for others, development of a useful screening process may be costly and very difficult. In addition, there are other, more important problems with reliance on artificially induced mutagenesis. It is impractical for long-lived plant species, and it cannot be employed successfully on higher (vertebrate) animals. Moreover, it can only produce practical results for traits controlled by the action of a single gene. Practically and theoretically, it is very difficult to induce and then select for multiple gene (polygenic) systems or dominant, single gene mutations—yet many economically useful traits within crop and livestock populations are determined by these genetic systems. Furthermore, it is impossible to induce and select for coadapted gene complexes, and their existence and economic value may be, in particular, one of the most important reasons for natural gene pool conservation. Coadapted gene systems, which have been created and are maintained by natural processes, may be transferred from crop or livestock germplasm resources to an advanced cultivar or breed through conventional breeding techniques; but induced mutations and human-directed selection cannot produce them artificially. Coadapted gene complexes have been documented in experimental populations of some fruit fly species. Considering economic biota *per se,* they have been suggested as the genetic basis for important environmental adaptations or economically useful traits in populations of oats, barley, wheat, rice, and tomato species. For example, it has been suggested that a coadapted gene complex may be responsible for the 'free-threshing Q factor'' which determines the loose glumes and tough rachis that distinguish the cultivated bread wheats from their wild and weedy relatives.

Most mutation breeders are aware of the irreplaceable value of natural sources of genetic variation, and they are acutely aware of the economic dangers which are inherent in the currently rapid destruction of the world's remaining natural reservoirs of genetic diversity. Considering what we presently do and do not know about the existence and economic significance of various gene combinations, including coadapted genes and polygenic inheritance, it would be very premature and foolhardy to suggest that we should delay at all in conserving our rapidly disappearing gene resources in favor of the optimistic claim that induced mutations can provide us with a satisfactory alternative. Moreover wishful thinking only serves to engender attitudes of complacency about the more urgent task at hand—that of salvaging samples of the natural genetic diversity which still remains on earth, and of finding some means for conserving portions of the traditional agro-ecosystems and natural areas that maintain and enhance these essential natural resources.

The immense value of both natural environments and traditional agro-ecosystems characterized by indigenous subsistence agriculture—as natural or *in situ* genetic reservoirs—dictates the proper conservation of unique and representative habitats of each. Within the United States, national programs for conservation of ecosystems and specific habitats with their biological resources and genetic materials intact include principally the National Park System of the National Park Service and the National Wildlife Refuge System, under the supervision of the U.S. Fish and Wildlife Service, U.S. Department of the Interior; the National Wilderness Preservation System; the Wild and Scenic River System; the marine sanctuaries program of the U.S. Department of Commerce; and the primitive areas within the National Forest System administered by the Forest Service of the U.S. Department of Agriculture. Privately supported conservation organizations such as the Nature Conservancy and Audubon Society also acquire and maintain natural areas for purposes of wildlife conservation. On the international level, the biosphere reserves program (Project No. 8) of UNESCO's Man and the Biosphere program has been coordinating a global network of reserves for all of the nations of the world, with each sponsoring country retaining control over and responsibility for the biosphere reserves within its own national boundaries. This international program is the only one that has thus far provided a rationale for conservation of economically and ecologically important habitats of both man-modified and natural areas.

We are urgently in need of a global conservation effort such as the World Conservation Strategy recently proposed by international conservation organizations (IUCN/UNEP/WWF, 1980). Global conservation will require the cooperation of numerous political entities, yet it will be important for all the peoples of the earth. Moreover, within each national boundary, there must be a sufficient commitment to both domestic and international conservation of genetic resources and the environments which sustain them. The United States has long been a world leader in economic development and technological progress—in part as a result of our search for and discovery of novel technological applications for a variety of genetic resources, and of our progress in developing *ex situ* conservation technology. The time has arrived for us to expand this role to include a focus on global *in situ* conservation of natural genetic reservoirs as well. If we fail to slow or halt the current wave of destruction and to effect adequate conservation of our renewable natural resources, we may be justifiably condemned by future generations of the earth for squandering both our genetic heritage and theirs.

2

Plant Resources and Food Production

One of our greatest challenges, and one that will intensify, is the widening gap between the world's growing human population and our present food production capabilities. While political and social leaders grapple with and attempt to control the problems created by population growth, scientists constantly seek new ways to increase agricultural productivity. Yet, future technological advances seem unlikely to give productivity results comparable to those of the past few decades: returns on crop yields are diminishing in proportion to technological input and energy costs continue to rise. The magnificent increases in crop yields that accompanied the advent of mechanized agriculture and energy intensive farming will probably not be repeated and may not even be sustained.

This outlook for agricultural productivity underscores the ever-increasing importance and value of agricultural genetic resources. We use gene resources agriculturally in two major ways: we choose certain species or populations to adopt for domestication or cultivation, and we genetically improve the most economically important of these through incorporation of gene resources. Since our returns on currently preferred crops are beginning to decrease in proportion to technological input, we should carefully scrutinize the unused potentials of our biotic support systems. We must begin to locate new sources of food and to find more efficient means of producing it by utilizing the wild, weedy, and primitive genetic resources related to our major crops and breeds. We must also take stock of the edible wild species that are now endangered or disappearing; we must develop the harvesting and management techniques necessary to retain these threatened species as renewable, food resource populations.

Today, as in the past, most of the world's human population is sustained by vegetable rather than animal foods. Of the estimated 350,000 plant species on earth, roughly a quarter (about 80,000 species) are believed to possess food value for

humans. Yet we have used only an estimated 3,000 species of these esculent plants (less than 4 percent!) and have commercially cultivated but 150 of these during the history of agriculture. Thus over the last 10,000 years, and particularly during the last century, we have significantly narrowed our agricultural food-producing options. Of the multitude of formerly cultivated plants and the plethora of available edible wild and weedy species, a mere handful have actually been adopted to feed most of the world's human population. Of the 30 major world crops cultivated in 1974, only seven—wheat, rice, corn or maize, potato, barley, sweet potato, and cassava—contributed annual harvests of at least 100 million metric tons each. The total tonnage of the remaining 23 crops was less than half that of these seven species. As the noted plant explorer and geneticist, J.R. Harlan points out:

> ...This is a relatively recent phenomenon and was not characteristic of the traditional subsistence agricultures abandoned over the past few centuries. As the trend intensifies, man becomes ever more vulnerable. His food supply now depends on the success of a small number of species, and the failure of one of them may mean automatic starvation for millions of people. We have wandered down a path toward heavy dependence on a few species, and there seems to be no return (1976a, p. 89).

Thus, we now utterly depend on the genetic integrity and continuing evolution of only a few crop plant species. For example, only three species—corn, wheat, and rice—now produce approximately two-thirds of the total world grain crop. Literally, "the fate of millions...hangs precariously on the balance of genetic systems between these three crops and their diseases and pests" (Timothy, 1972, p. 2).

So much time and energy have been invested in the genetic improvement of the most highly productive or major crop (and livestock) species, that they have gradually displaced a great number of the relatively unimproved, "minor" crops. Today, many of these minor food species are disappearing or are in danger of extinction, e.g., primitive leguminous crops such as tarwi (*Lupinus mutabilis*), the swordbean relatives, *Canavalia plagiosperma* and *C. regalis*, and the African yeheb nut (*Cordeauxia edulis*). Such impending losses are unfortunate because the minor crops have also been genetically improved in comparison with their wild ancestors as have the more modern cultivars. Many of them could be further improved and used to extend significantly the present range of agricultural production, especially in food-poor regions of tropical or arid climates. Moreover, minor food resources often possess unique nutritional, culinary, taste, or other properties that are lacking in our major crop species.

In addition, there are also a great number of endangered or extinct wild food resources. Aside from the wild or weedy species that have been entirely or nearly extinguished as a result of humanity's quest for food, a number of the wild progenitors or ancestors of our domesticated favorites are also threatened or have been irretrievably lost. One such example is that of the threatened forms of teosinte (*Zea spp.*), a weedy plant which may be the wild ancestor of corn (*Zea mays*) and certainly has influenced its evolution. Within the United States and its territories, more than 160 wild relatives of crops and 150 relatives of forage plants have been listed as endangered or threatened taxa which may be eligible for protection under the Endangered Species Act of 1973. Conservation of gene pools of wild crop resources is not merely an exercise prompted by historical interest. Wild species are important as sources of genes and genetic information necessary for the continuing evolution and genetic improvement of our preferred domesticates. Without these gene resources and the environments in which they were created and are maintained, millions of

dollars of agricultural produce derived from major crop species would be lost each year in the United States alone.

Why would such losses occur? Because most industrialized economies encourage monocultures of crop species, as do many of the developing nations in their more recent attempts to enhance their agricultural productivity. In monocultural agro-ecosystems a single food species is cultivated (to the exclusion of others) over large tracts of farmland. These modern agro-ecosystems typically require high inputs of energy, fertilizers, pesticides, water, and high-yielding, genetically uniform seed stocks. As a result, these systems are capable of producing more food at less cost to consumers, but they are usually much more vulnerable to severe outbreaks of diseases and pests or other problems because of their almost exclusive reliance on one or a few genetically uniform cultivars of the same crop species. In the past, primitive and especially wild gene resources were used infrequently in the genetic improvement of our modern cultivars, but their role has become increasingly important. Wild, weedy, and primitive relatives of economic species are important for studies of the evolutionary histories of crops. These studies facilitate our ability to use various germplasm resources to alter the genetic constitution of our economic crop plants. More important, wild or primitive resources are frequently employed directly in the crop improvement process—a role which has increased rapidly in recent years.

For example, consider the wild gene resources of wheat (*Triticum aestivum*), one of the world's most important staple food crops. Two factors severely limit current efforts to improve modern wheat cultivars and extend their range of cultivation: (1) the extinction of valuable wild or weedy relatives needed as germplasm resources in wheat improvement programs; and (2) the fact that most of the conserved stocks of cultivated wheat gene resources have already been exploited fully in past genetic improvement programs. The combined effect of overuse of available genetic materials and extinction of the gene resource populations that remain in natural environments and traditional agro-ecosystems is resulting in disastrous economic consequences. The world wheat crop has become increasingly vulnerable to old and new diseases and pests and to adverse climatic conditions. This situation, which is the same for the majority of the most important world crops, has been summarized by two wheat geneticists:

> The failure to conserve the primitive cultivated varieties of wheat has already resulted in the loss of a substantial reserve of genetic variability. Attempts to increase the variability of the new cultivated wheats by inducing mutations, either by ionizing radiation such as X rays or by chemical treatment, have met with little success. Conservation of the germplasm of the surviving primitive cultivated wheats can lessen the danger of further genetic erosion. On a large scale, however, the restoration and enrichment of the gene pool of the cultivated wheats can be accomplished only by tapping the vast genetic resources that are to be found in the wild relatives of the wheats (Feldman and Sears, 1981, p. 102).

As these researchers point out, the modern varieties of wheat have been improved at the expense of these conserved genetic resources, yet the genetically uniform, modern varieties created by this process have steadily replaced the remaining primitive and wild gene resources needed for future wheat improvement efforts.

In short, we have both reduced the species diversity in our agricultural production systems, and narrowed the intraspecific genetic diversity available for the improvement of our economically preferred crop species. The attrition of both wild and minor crop species and the disappearance of the once bountiful reservoirs of

wild and primitive germplasm resources are perhaps the most unfortunate consequences of the adoption of recent agricultural practices. A reversal of this trend is necessary if we are to provide adequately and effectively for our own future and to enhance our genetic endowment for increasing food resource options for future generations. We can genetically improve extant economic species, we can domesticate new crop (and livestock) species, and we can rediscover and improve minor crops. But these goals cannot be accomplished without more effective conservation and greater use of wild and primitive genetic resources (see Appendix).

Genetic variability undergirds the success of every genetic improvement process. The improvement of any edible species is ultimately limited by the availability of genetic diversity within its populations and the techniques that have been developed for the manipulation and incorporation of useful genes or gene complexes from related species. Technically, we are merely continuing the domestication and crop improvement efforts that our ancestors began many thousands of years ago. The primary difference is that today the improvement process proceeds much more rapidly because we have enhanced our knowledge of the evolutionary histories and genetic structures of our crop species. Our accumulated knowledge in concert with our improved technological capabilities has immensely facilitated the use of our genetic heritage. As long as sufficient genetic variability is available, those processes may continue; and conservation of gene pools of wild food species and primitive as well as modern crop populations is the principal means to accomplish this aim.

The Economic Importance of the Centers of Crop Genetic Diversity

With the exception of a very few minor crops, the entire U.S. agricultural production network is based on nonnative, introduced plant and animal species. Moreover, the continuing success of the agricultural sector of our economy is dependent on the genetic integrity of these species. Their economic value, and the value of the gene resources which must be imported to sustain them, is tremendous. For example, in 1975 crop seed and live animal stocks of our introduced domesticates provided to farmers and ranchers by the genetic supply industry in the United States were valued at more than $2.85 billion. The value actually added to this essential agricultural industry from the use of genetically improved seed and animal stocks was estimated at nearly $1.6 billion, and almost $1.15 billion for crop seed stocks alone. Even though virtually all of this basic productivity is ultimately derived from introduced genetic materials, only a portion of it can be attributed to wild or primitive gene resource stocks. A reasonable estimate of the contribution of such germplasm resources to the genetic supply industry alone is at least 10 percent—or $160 million, while a very conservative estimate would place the value of these resources at $16 million (1 percent). For improved crop seeds, the analogous figures would be $114 million and $11.4 million. When one considers the value of the food derived from the use of genetically improved crops (and livestock), the contribution of wild and primitive genetic stocks becomes magnified many times over. However, it is difficult to arrive at a suitable estimate of the value of this agricultural productivity; for example, even though a genetic resistance factor from a wild species may allow protection of a crop

variety in a particular agricultural environment, it will be responsible for only a portion of the productivity of the variety in those years in which the weather and other environmental conditions are suitable for a disease epidemic. In short, no long-term, carefully constructed studies have been conducted to determine the economic contribution of this or that wild-derived gene; but the annual crop productivity dependent on genetic materials obtained from wild and primitive crop gene resources is surely in the hundred million dollar range. It is commonly acknowledged that the value of these gene resources relative to those obtained from modern or obsolete cultivars, has increased significantly in recent years.

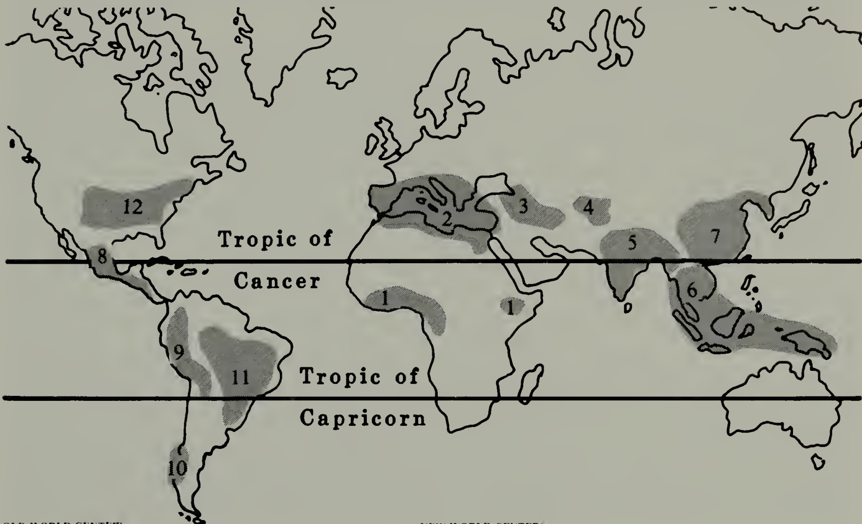
Thus, introduced gene resources constitute the biological basis of the agricultural production system of the United States as well as those of all other modern, industrialized societies. The gene pool resources of the world's crop species exist in identifiable areas called ''crop gene centers'' (Fig. 1). These regions contain both the natural habitats of the wild ancestors of our crops and the traditional agro-ecosystems in which most of our domesticated plants originated and became genetically diversified. During the last half century, development within these regions has accelerated tremendously. The natural habitats and traditional agricultural systems that have maintained the world's wild and primitive gene resources for thousands of years are now being increasingly converted to urban, industrial, or other more intensive forms of land use. More important, during the last few decades the technologies characteristic of the Green Revolution and other agricultural practices associated with monocultures of genetically uniform but high-yielding seed stocks have also had a detrimental effect on the survival of valuable gene resource populations. The prevailing trend has been the replacement of genetically diverse resource populations with these ''improved'' but highly uniform crop populations. This has not only resulted in some genetically based epidemics with concomitant reductions in crop productivity, but it has also contributed greatly to the attrition of valuable crop gene resources.

Genetically diverse primitive crop cultivars (Fig. 2) together with their supportive wild and weed relatives, provide both genetic stability for traditional agro-ecosystems in developing nations and valuable genetic resources essential for the survival of technologically advanced agricultural systems in industrialized nations. The widespread and extensive loss of these resources and their requisite habitats has become so alarming that the recently formed International Board for Plant Genetic Resources (IBPGR) has designated priority crops and regions urgently in need of collection of crop germplasm for *ex situ* conservation. The IBPGR priority ratings of major world crops, and the areas most in need of collection of these gene resources, are listed in Table 1. It is important to note that the areas most urgently in need of collection are situated within the world crop gene centers.

The Link Between Modern and Traditional Agricultural Systems

In the absence of a constant supply of gene resources from these areas, modern agro-ecosystems typical of the monocultures in the United States would not be nearly as productive as they are today. In fact, the latter would probably not even exist in their present form. One reason for this is that natural sources of genetic diversity from crop gene centers cannot be replaced by exclusive reliance on artificially induced

PRESUMED GENE CENTER OF MAJOR WORLD CROP PLANTS



OLD WORLD CENTERS

1. ETHIOPIA-WEST AFRICA
   - Barley
   - Arabica coffee
   - Cowpea
   - Oil palm (African)
   - Okra
   - Onion
   - Rice (African)
   - Robusta coffee
   - Sesame
   - Sorghum
   - Yam

2. MEDITERRANEAN
   - Asparagus
   - Beets
   - Cabbage
   - Carob
   - Chicory
   - Hops
   - Lettuce
   - Oats
   - Olive
   - Parsley
   - Parsnip
   - Radish
   - Rhubarb
   - Strawberry (European)
   - Wheat

3. ASIA MINOR
   - Alfalfa
   - Almond
   - Apricot (secondary)
   - Barley
   - Beets (secondary)
   - Cabbage
   - Cherry
   - Chickpea
   - Date palm
   - Carrots
   - Fig
   - Grapes
   - Lentils
   - Oats
   - Onions (secondary)
   - Pea
   - Pear
   - Pistachio
   - Pomegranate
   - Rye
   - Safflower
   - Wheat

4. CENTRAL ASIATIC
   - Almond
   - Apple
   - Apricot
   - Broad bean
   - Cantaloupe
   - Carrots
   - Chick pea
   - Grapes *(Vitis vinifera)*
   - Lentils
   - Mustard
   - Onion
   - Pea
   - Pear
   - Sesame
   - Spinach
   - Turnips
   - Wheat

5. INDO-BURMA
   - Amaranths
   - Cucumber
   - Eggplant
   - Lemon
   - Mango
   - Millets
   - Orange
   - Pepper (black)
   - Rice
   - Sugar cane
   - Taro
   - Yam

6. SIAM, MALAYA, JAVA
   - Aroids
   - Banana
   - Betel palm
   - Breadfruit
   - Clove
   - Coconut
   - Ginger
   - Grapefruit
   - Sugar cane
   - Mangosteen
   - Nutmeg
   - Rice (Asian)
   - Yam

7. CHINA
   - Adzuki bean
   - Apricot
   - Buckwheat
   - Cinese cabbage
   - Cowpea (secondary)
   - Millets
   - Oats (secondary)
   - Mandarin Orange
   - Peach
   - Radish
   - Rhubarb
   - Soybean
   - Tea

NEW WORLD CENTERS

8. MEXICO-GUATEMALA
   - Allspice
   - Amaranths
   - Avocado
   - Beans *(Phaseolus vulgaris)*
     (Phaseolus multiflorus)
     (Phaseolus lunatus)
     (Phaseolus acutifolius)
   - Corn
   - Cacao
   - Cashew
   - Guava
   - Papaya
   - Pepper (green)
   - Sapodilla
   - Squash
   - Sweet potato
   - Tomato
   - Vanilla

9. ANDES
   (PERU-ECUADOR-BOLIVIA)
   - Amaranth
   - Bean *(P. vulgaris)*
     (P. lunatus)
   - Cacao
   - Corn (secondary)
   - Edible roots
     (oca, ullucu, arracacha, anu)
   - Guava
   - Papaya
   - Peanut
   - Pepper (red)
   - Potato (many species)
   - Quinoa
   - Squash *(Cucurbita maxima)*
   - Tomato

10. SOUTHERN CHILE
    - Potato (Chilean)
    - Strawberry (Chilean)

11. BRAZIL-PARAGUAY
    - Brazil nut
    - Cacao (secondary)
    - Cashew
    - Cassava
    - Maté
    - Oil palm (American)
    - Peanut (secondary)
    - Pepper (red)
    - Pineapple

12. UNITED STATES
    - Sunflower
    - Blueberry
    - Cranberry
    - Jerusalem artichoke
    - Strawberry (American)

Fig. 1. Each modern crop plant originated and diversified in a particular geographic region; today these regions are known as world crop gene centers. The major world gene centers, first recognized by the Russian plant explorer and breeder V.I. Vavilov in the 1920's, are now rapidly disappearing. (Illustration: After: H.G. Wilkes; Bulletin of the Atomic Scientists)

Fig. 2. A field in central Greece (part of the Mediterranean crop gene center) planted with 'Mavraghani,' an improved local (primitive) variety of wheat. (Photo: United Nations Food and Agriculture Organization)

TABLE 1. Endangered or Threatened Crop Genetic Resources: Collection Priorities for Major World Crops*

Crop	Priority Rating and Region(s) Where Collection is Needed
Cereal Crops:	
Wheat	(1) Mediterranean; Ethiopia; S.W. & Central Asia.
Sorghum	(1) Ethiopia; Africa (So. of Sahara); So. Asia; Far East.
Pearl millet	(1) Africa (esp. south of the Sahara).
Rice	(1) South & S.E. Asia (Asian); West Africa (African).
	(2) Central Asia; Far East; East Africa.
Barley	(1) Southwest Asia; North Africa.
	(3) Far East; Central Asia; Ethiopia.
Millets (Other)	(2) South Asia; Far East; Ethiopia; East Africa.
Maize/Corn	(3) All regions except S.W. Asia & Pacific Islands.
Oats and Rye	(3) S.W. & Central Asia; Mediterranean.
Legume Crops (Pulses):	
Phaseolus beans	(1) Mexico; Caribbean Islands; Andes; Spain & Portugal.
	(2) Chile, Ecuador & Galapagos Islands.
Peanut/Groundnut	(1) Meso-America; Indo-Burma; Caribbean Islands.
	(2) West Africa.
Soybeans	(2) Far East; S.E. Asia; E. Africa; Ethiopia.
Chickpea/Garbanzo	(2) Mediterranean; South, S.W. & Central Asia; Ethiopia.

TABLE 1. (Continued)

Crop	Priority Rating and Region(s) Where Collection is Needed
Cowpea (African *Vigna*)	(2) Ethiopia; East & West Africa.
Cowpea (Asiatic *Vigna*)	(2) South & Central Asia; Far East; Brazil.
Pea	(3) Mediterranean; S.W. & Central Asia; Ethiopia.
Pigeonpea	(3) South & S.E. Asia; East Africa; Meso-America.
Field bean	(3) South, S.W. & Central Asia; Mediterranean; Ethiopia.
Root & Tuber Crops:	
Potato	(1) Mexico; Andes; Central America.
	(2) Brazil; Guatemala; U.S.; parts of South America.
Sweet Potato	(2) Pacific Islands; S.E. Asia; Meso-America; Andes; Brazil; southern South America.
Cassava/Manioc (Tapioca)	(2) South & S.E. Asia; Far East; E. & W. Africa; Brazil; southern South America; Meso-America.
Yam	(3) South & S.E. Asia; E. & W. Africa; Far East; Brazil; Meso-America; Pacific Islands.
Vegetable Crops:	
Tomato	(1) Andes; other areas not yet specified.
Onions	(1) Not yet specified.
Amaranths	(1) Indo-Burma; Africa; Meso-America; Andes; S.E. Asia; China.
Brassicas**	(1) Not yet specified.
Peppers	(1) Meso-America (Mexico); Andes (esp. Peru).
Cucurbits (squashes, gourds, pumpkin)	(1) Meso-America; South America; regions for most species not yet specified.
Eggplant	(1) Africa; S.E. Asia & other parts of Asia.
Okra	(1) West Africa.
Cucumber	(2) Not yet specified
Cantaloupe/Muskmelon	(2) Not yet specified.
Watermelon	(2) Not yet specified.
Carrot	(2) Not yet specified.
Lettuce	(2) Not yet specified.
Radish	(2) Not yet specified.
Peas	(2) Not yet specified.
Winged bean	(2) Not yet specified.
Fruit & Nut Crops:	
Bananas & Plantains	(2) Pacific Islands; Far East; South & S.E. Asia; Ethiopia; East Africa.
Fruit & Nut trees	(S) Tropical plants and their habitats will be preferred over temperate plants; most not yet specified.
Edible Oil Crops:	
American oil palm	(2) Brazil; Meso-America.
African oil palm	(3) West Africa.
Rapeseed *(Brassica)*	(3) South & S.W. Asia; Far East; Ethiopia; Meso-America.
Olive	(3) Mediterranean; S.W. Asia.

TABLE 1. (Continued)

Crop	Priority Rating and Region(s) Where Collection is Needed
Safflower	(3) Mediterranean; South, S.W. & Central Asia.
Sunflower	(3) United States; Meso-America; Ethiopia; Central Asia.
Sugar Crops:	
Sugar beet	(1) Mediterranean (Central & East).
	(2) Mediterranean (West).
	(3) Atlantic Islands.
Sugar cane	(2) South, S.E. & Central Asia; Far East; Pacific Islands.
Beverage Crops:	
Coffee	(1) Ethiopia; Sudan
	(2) W. & Central Africa; Uganda; Mozambique; N.&S. Yemen.
	(3) Madagascar; East Africa.
Grape	(1) Indo-Burma; China; USSR; Asia Minor.
	(2) S.W. Asia; Mediterranean (So.); Caribbean Islands.
	(3) N.&S. Yemen; Ethiopia; Egypt; United States; Mexico.
Cocoa	(2) Meso-America; Brazil.
Forage Grasses:	
Bermudagrass *(Cynodon)*	(1) Africa (star grass; bermuda).
	(2) Asia; Mediterranean.
Panicums *(Panicum)*	(1) Africa (guineagrass; paragrass).
	(2) Asia (common millet).
Foxtail millet *(Setaria)*	(1) Africa.
	(2) Asia.
Brachiaria millet	(1) Africa.
Pennisetum millets	(1) Africa (elephant grass; kikuyu grass).
	(2) Asia.
Crabgrass *(Digitaria)*	(1) Africa—southeast (pangola grass).
Bluestem *(Andropogon)*	(1) Africa (gamba grass).
Rhodesgrass *(Chloris)*	(1) Africa.
Lovegrass *(Eragrostis)*	(1) Africa.
Buffel grass *(Cenchrus)*	(1) Africa.
	(2) Asia.
Paspalums *(Paspalum)*	(2) South America (dallis grass; bahia grass; vaseygrass).
Carpetgrass *(Axonopus)*	(2) South America.
	(3) Meso-America.
Tripascum *(Tripsacum)*	(2) South America.
	(3) Meso-America.
Bromegrass *(Bromus)*	(2) Mediterranean; Europe; temperate South America.
Wheatgrass *(Agropyron)*	(2) Mediterranean.
Ryegrass *(Lolium)*	(2) Mediterranean; Europe.
Fescues *(Festuca)*	(2) Mediterranean; Europe.
Timothy grass *(Phleum)*	(2) Europe.
Reed canarygrass *Phalaris)*	(2) Mediterranean.
Orchardgrass *(Dactylis)*	(2) Europe.
Bluegrass *(Poa)*	(2) Temperate South America.

TABLE 1. (Continued)

Crop	Priority Rating and Region(s) Where Collection is Needed
Forage Legumes:	
Alfalfa *(Medicago)*	(1) Mediterranean; Europe; S.W. Asia.
	(2) So. Australia (annuals); Mediterranean (temperate).
Clovers *(Trifolium)*	(1) Europe; S.W. Asia; Mediterranean (tropical).
	(2) E. Africa; So. Australia; Mediterranean (temperate).
Lucernes *(Stylosanthes)*	(1) Tropical South America; Meso-America.
	(2) Tropical Asia.
Desmodiums *(Desmodium)*	(1) Meso-America; tropical South America.
	(2) Tropical Asia.
	(3) Australia.
Desmanthus *(Desmanthus)*	(1) Meso-America.
Groundnuts *(Arachis)*	(1) Tropical South America.
Common beans *(Phaseolus)*	(1) Meso-America; tropical South America.
Butterfly pea *(Centrosema; Clitoria)*	(1) Meso-America; tropical South America *(Centrosema)*.
	(2) E. Africa *(Clitoria)*.
Leucaena *(Leucaena)*	(1) Meso-America; tropical South America.
Vetches *(Vicia)*	(1) Europe; Mediterranean; S.W. Asia.
Sweet clover *(Melilotus)*	(1) Europe; Mediterranean.
Sanfoin *(Onobrychis)*	(1) Europe; Mediterranean; S.W. Asia.
Soybeans *(Glycine)*	(2) E. Africa; tropical Asia.
	(3) Australia.
Cowpeas *(Vigna)*	(2) E. Africa; tropical Asia.
	(3) Australia.
Lablab *(Dolichos)*	(2) E. Africa.
Kudzu *(Pueraria)*	(2) Tropical Asia.

*Collection priorities for some minor food and forage crops have been omitted, as have all fiber crop species. Priority 1 = crops and regions most urgently in need of collection, and priorities 2, 3, and 4 are used to indicate descending order of importance for collection. Priority 4 crop genetic resources—those of lesser importance—have also been omitted. Priority S indicates further study is necessary before a priority rating can be assigned.

**Brassicas *(Brassica* spp.) considered here include cabbages, kales, mustards, collards, Brussels sprouts, broccoli, cauliflower, and kohlrabi.

Sources: Consultative Group on International Agricultural Research (CGIAR). 1976. *Priorities Among Crops and Regions.* Rome: International Board for Plant Genetic Resources (IBPGR).
IBPGR. 1979. *A Review of Policies and Activities 1974-1978 and of Prospects for the Future.* Rome: IBPGR Secretariat.
IBPGR. 1980. *Annual Report 1979.* Rome: IBPGR Secretariat.
IBPGR. 1981. *Annual Report 1980.* Rome: IBPGR Secretariat.

mutations. When the available gene resources that have been collected and stored have been exhausted, induced mutations will not be able to produce sufficient genetic diversity to meet changing needs fast enough. Secondly, *ex situ* conservation methods, such as gene banks, do not provide a panacea for conserving natural sources of crop genetic diversity. Storage of seeds involves the freezing of evolutionary processes, and new types or levels of genetic resistance cannot evolve in such stored populations because they cannot respond to the selective pressures of mutating pest or pathogen populations. By maintaining some environments where such adaptive processes can continue, i.e., *in situ* conserved natural areas and traditional agro-ecosystems and *ex situ* mass reservoirs, we can capitalize on the "free work" of nature. This will occur as long as resource populations consisting of sufficient numbers of individual organisms and their natural or man-modified habitats are properly maintained.

The major reason for the genetic, and hence economic, vulnerability of the U.S. agricultural production system is that our modern agro-ecosystems have been fashioned by economic principles which have, as their primary goal, the maximization of present production. In order to maximize productivity, crop populations must be highly genetically uniform. As the National Academy of Sciences' (NAS) Committee on Genetic Vulnerability of Major Crops (1972) has pointed out, U.S. consumers demand agricultural produce of a uniform quality. The impact of consumer demand is transferred to the farmers who, in turn, demand uniformity in order to increase their production efficiency per unit area or per hour:

> Demands for efficiency are really demands for uniformity in a different guise. The farmer must have high-yielding varieties. Because the low-yielding members of the plant population have been eliminated, this too means uniformity. The farmer must substitute machines for men, but machines can't think, again varieties must be uniform.
>
> Seeds are sown by machine. These too must be uniform or they move unevenly and inefficiently through the planter. The seeds must germinate and grow simultaneously, or they leave space for weeds to grow in the row where the cultivating machine cannot go.
>
> Crops must be uniform for harvesting. Tomatoes, peas and potatoes must ripen at the same time if they are to be machine harvested, because the machine cannot distinguish between a green tomato and a ripe one.
>
> And so it goes, uniformity—always uniformity (NAS, 1972, p. 289).

Thus, in an economic sense genetic uniformity is a useful and necessary strategy for enhancing crop productivity. However, when relied on exclusively, as it has been all too often in the past in the United States, uniformity sets the stage for genetically based epidemics of crop pests and diseases. Most of the crop acreage in the United States is planted in only one or a few genetically uniform varieties of each of the major crops. And genetic uniformity is related to, and in many cases equivalent to, genetic vulnerability to disease or pest attack. The 1970 southern corn leaf blight epidemic, caused by the pathogen *Helminthosporium maydis (=Bipolaris maydis)* is merely one example of the potentially disastrous consequences of relying on highly uniform crop populations (Fig. 3). This epidemic highlighted the vulnerability of major crops in the United States to pest attack and eventually precipitated the 1972 NAS report. It affected thousands of acres of 'Texas T cytoplasm' corn—a male-sterile corn variety which decreased the costs of producing higher-yielding, hybrid corn varieties by eliminating the need for manual "detasseling." By 1970, roughly three-fourths of the crop acreage in the United States was planted in this one variety. When the blight struck, the result was an estimated $1 billion loss—a reduction in

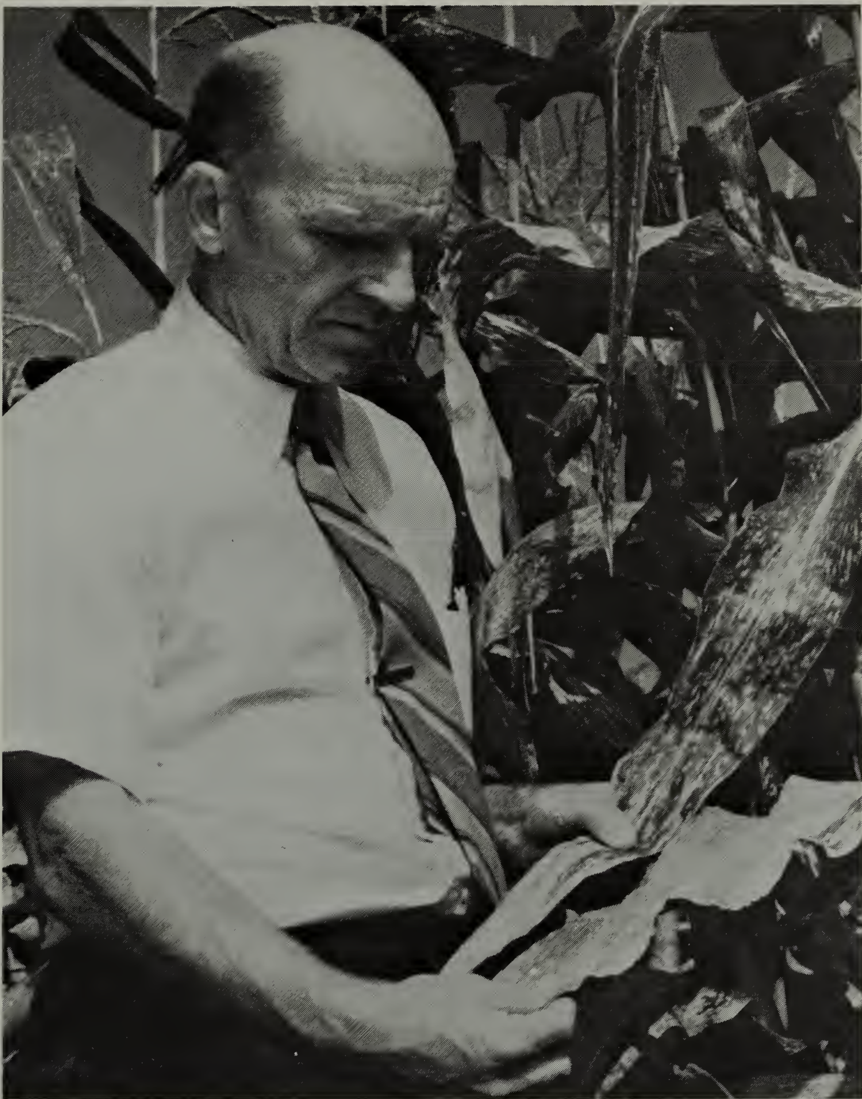


Fig. 3. A researcher examining the effects of southern corn leaf blight. In 1970 a new race of this blight caused an estimated $1 billion loss of the U.S. corn crop. (Photo: USDA)

productivity of approximately 710 million bushels of corn. But this was not the first genetically based epidemic experienced by the United States or other nations. Red rust destroyed 3 million bushels of wheat in the United States and Canada in 1916, resulting in at least 2 wheatless days each week in the United States in 1917. The U.S. wheat belt was affected again by rust epidemics in 1935 and 1953. Even the Irish and European potato famines of the 1840's were genetically based epidemics. The Irish

potato blight alone resulted in the death of an estimated 1-2 million people and the emigration, primarily to the United States, of 2 million more people. The remaining Irish population of approximately 2-4 million was left in abject poverty. The potato blight, caused by the disease pathogen *Phytophthora infestans,* was precipitated by the extensive planting of the 'Lumper' variety—a genetically uniform potato cultivar which was susceptible to the pathogen.

Each time such epidemics have occurred, plant breeders have had to turn to stored stocks of crop gene resources, primarily those derived from the gene centers, to correct the situation. For example, during the 1970 southern corn leaf blight epidemic, intensive studies were launched to locate sources of resistance genes as well as alternative genes for male sterility. Conserved seed stocks were analyzed and several corn strains that carried the necessary resistant genetic material were located. The USDA Research Service and state agricultural experiment stations cooperated in an effort to analyze the available crop strains containing genetic resistance. Subsequently, the most promising genetic materials were supplied to the seed industry (part of our genetic supply industry) for incorporation into the vulnerable but high-yielding hybrid corns. Many crop varieties, e.g., some of the modern wheats, have been routinely retired from use in order to upgrade their genetic resistance to their ever-present diseases and pests.

A great multitude of wild or weedy crop relatives and primitive cultivars have been essential in the development of improved varieties. Some of these have actually rescued entire plant industries from the brink of economic disaster. The application of plant breeding techniques for production of genetically resistant crops began around 1870—100 years prior to the corn leaf blight epidemic. At that time the French grape and wine industry was saved by native American grape varieties. These grapes were scarcely different from their wild ancestors. Like their wild relatives, they were resistant to the devastating grape root plant louse (*Phylloxera* spp.)—which was accidentally introduced to France from the United States. Once introduced to Europe in 1860, the *Phylloxera* plant lice rapidly spread throughout the genetically susceptible grape populations. Eventually, the entire grape-growing region of Europe was affected. The French grape industry was first sustained by resistant American grape rootstocks (used for grafting). Later, nearly immune hybrids were developed by crossing the old French varieties with the more vigorous, disease-resistant American plants.

The centers of crop genetic diversity harbor a vast array of genetic resources and have long been the traditional source of useful genes for crop improvement programs. They have historically provided the primary sources of genotypic resistance to crop insect pests, disease pathogens (such as fungi), and nematodes. As the late plant breeder and taxonomist, Dr. E.E. Leppik (1970) has commented: "...the use of resistant cultivars is the only applicable method of control in many cases of highly specialized parasites, such as rusts, soil-borne smuts, and certain nematodes..." (p. 323). For example, many primitive cultivars of West African rice have been used as sources of resistance to extremely virulent races of rice blast. The information already available on the use of wild and weedy crop relatives is enormous. Wild and weedy species have added essential germplasm resources to the conserved gene pools of important annual crops in the United States, particularly those which tolerate "wide crosses" with their wild relatives. Examples include wheat, potato, rice, sugarcane, cotton, tomato, tobacco, and many fruits. For example, modern wheat

cultivars have received disease resistance genes from wild relatives, such as *Agropyron* spp. Furthermore, the use of wild-derived rootstocks for commonly grafted species, such as grape, citrus, peach, and pistachio, has often solved serious pest and disease problems. Improved forage grasses used to enhance livestock production have also profited from the incorporation of resistance genes from wild species. Indeed, some of our most important crops "...could not maintain commercial status without genetic support of their wild relatives" (Harlan, 1976c, p. 330).

Additionally, wild, weedy, and primitive germplasm resources have also been utilized for a host of other adaptations. A prominent concern has been that of extending the present range of adaptation of preferred agricultural species. This is usually achieved through the location and incorporation of genes that control tolerance of either inadequate or excessive rainfall or humidity, heat, cold, and saline or other adverse soil conditions, and genes that confer resistance to pests and diseases. Other uses of crop gene resources include: increases in yield, uptake of fertilizers or water, improved photosynthetic efficiency, earliness, thornlessness (in cultivated bramble fruits), other alterations in storage or harvesting properties, and improvements in nutritional value. Breeding for dwarf stature—one of the most important characteristics of the modern high-yielding varieties—has also been achieved in wheat through the use of wild *Agropyron* derivatives. It has even been suggested that in the near future germplasm from crop weed relatives may be used to transfer herbicide resistance to cultivated crop varieties.

Notwithstanding, the major world gene centers are not the only habitats that provide useful genes for crop improvement programs. Genetically determined traits have been located in habitats not known to be affected by the environmental stress for which the trait was deemed useful. For example, flood-tolerant rice cultivars were unexpectedly identified from a collection adapted to areas not historically affected by floods. Similar observations have been made for disease and pest resistance genes, e.g., all of the 190 strains of African rice (*Oryza glaberrima*) tested so far have shown high levels of resistance to the rice green leafhopper, yet this devastating rice pest has never been observed in West Africa, the presumed native habitat of African rice. Many other examples have been provided of useful resistance factors which apparently arose in the absence of the specific crop predator or pathogen for which each has been employed to combat.

Gene Centers and the Origin of Crops

Since the advent of modern (post-Mendelian) breeding practices at the turn of this century, we have made great strides in the genetic improvement of our domesticated crops. However, in spite of these advances, our primary food (and fiber) resources have changed only slightly. With few exceptions, the major crops of modern times are of ancient origin. Most were domesticated before the time of Christ, and were staples of agricultural peoples long before recorded history. All domesticated food species were wrested from the wild—a process which began around 10,000 B.C. in regions often referred to as "hearths of domestication."

For example, consider the origin of the modern wheats (*Triticum* spp.), which together now comprise the most important staple food for 35 percent of the world's people or more than 1 billion people. Wheat domestication initiated in the hilly country flanking the Syrian desert and Tigris-Euphrates plain of ancient Mesopotamia. This

area is southwestern Asia, called the Fertile Crescent, is the geographical center for the wild wheats which provided the three basic genomes of our modern wheats. The source of one genome (A), wild einkorn *(T. monococcum),* although far less abundant than in the past, currently enjoys a more or less continuous distribution throughout the steppes and open habitats of the native oak forests of the Fertile Crescent. Einkorn was later domesticated and used as a primitive cultivar in Turkey. Another genome (B) was probably derived from the domesticated form of wild emmer wheat (*T. turgidum* var. *dicoccoides*), which most likely acquired the B genome from *T. searsii* or another wild wheat species. The wild progenitor of the once widely cultivated emmer wheat occupies essentially the same natural habitats as wild einkorn. The modern durum wheats (*T. turgidum* var. *durum*) descended from a mutant emmer. The third genome (D) was derived from wild goat grass (*T. tauschii* or *Aegilops squarrosa*) which grows naturally along the edges and within traditional wheat fields in Iran and Armenia. Today natural hybrids between this wild species and primitive wheat cultivars can still be readily located there. Thus, from the three wild grasses, we have obtained the basic genetic constitution of our modern durum (AB) and bread (ABD) wheats.

The oak and pistachio woodlands of the Near East are also the ancestral home of the wild progenitors and early domesticates of barley (*Hordeum*), peas (*Pisum* and *Cicer*), lentils (*Lens*), forage legumes (*Vicia*), and other ancestors of southwest Asia's staple crops. Similarly, the mesquite groves in the Mexican highlands are the home of many races of teosinte, *Zea mexicana (Euchlaena mexicana),* the closest relative of corn (*Zea mays*) (or a descendant thereof). In natural areas such as these, the genetic constitutions of the wild ancestors of our domesticates were shaped by interactions with their environment over long periods of time. In addition to the various abiotic environmental factors (e.g., wind, temperature, rainfall), other wild species (biotic factors) have played an essential role in the evolution of important adaptations possessed by wild progenitors. Many of these adaptations are still present in the crops that have descended from them, e.g., the reproductive anatomy or floral parts of crop species. Some crops, especially grasses such as corn and wheat, inherited floral characteristics adapted for pollination by the wind, an abiotic factor. However, others, including many fruit, nut, and leguminous forage crops, inherited the floral morphology of their progenitors which adapt them to insect pollination.

Many other essential genetically determined traits became part of the genetic constitution of our cultivated species during the domestication process. An excellent example is that of the "nonshattering" and "free-threshing" traits which have facilitated the cultivation of grain crops. Nonshattering grain plants do not release their grain heads or spikes at maturity, so that both the stalks and spikes can be harvested simultaneously. Harvested nonshattering grain plants that are also free-threshing have seed grain that can be easily removed from the hulls by threshing and winnowing. These inherited traits were obviously selected by man from plants in wild and cultivated populations, since plants that have brittle fruiting stalks and persistent grains are better adapted to survival in the wild. In general then, the genetic make-up of domesticated crop species has been influenced by selective pressures wrought by man in addition to those imposed by natural and man-modified environments. The natural environments that provided the wild species from which our crops originated still harbor these valuable crop genetic resources.

As crops were domesticated and spread from one major agricultural region to another, gene centers—areas marked by high levels of crop genetic diversity—became more clearly defined. Gene centers were intimately associated with traditional agricultural systems:

> . . . traditional agriculture generated enormous diversity in identifiable geographic regions called "centers of diversity" or "gene centers." Such centers are (or were) found on every continent except Australia where the native people did not cultivate plants. Wherever they are located they are always characterized by (i) very ancient agriculture, (ii) great ecological diversity (usually mountainous regions), and (iii) great human diversity in the sense of numerous culturally distinct tribes with complex interacting histories (Harlan, 1975c, p. 618).

The crop gene centers we recognize today (Fig. 1) are still associated with areas where people practice ancient or premodern farming methods. The formation of these agro-ecosystems and the production of surplus food were necessary prerequisites for the establishment and maintenance of the first human civilizations. However, the essential role of these ancient regions of traditional agriculture has changed very little over the centuries. From the ancient civilizations of Mesopotamia and the Nile Valley to our modern, industrialized societies, each agricultural system has been based primarily on crops and genetic materials obtained from the world gene centers. Today, primitive crop cultivars from these areas are still being introduced for use in modern agro-ecosystems. The introduction of 'Argentine,' a primitive peanut cultivar from the province of Entre Rios in Argentina (see gene center #11 in Fig. 1), resulted in an estimated $9.4 million annual increase in productivity to U.S. growers between 1963 and 1968. In addition, foreign habitats associated with crop gene centers are still our primary sources of wild and primitive germplasm resources for improvement of established crops.

In addition to fostering the growth of more complex human aggregations, traditional agro-ecosystems provided essential habitats for the evolution of the newly domesticated plant types and primitive cultivars. Under the selective pressures imposed by nature and by man and his agricultural environments, the early crop plants diverged even further from their wild ancestors. Yet despite genetic divergence, occasional crosses occurred between the primitive crops and their wild relatives. During the course of domestication, selection among the genetically diverse hybrids of these crosses allowed the incorporation of disease and pest resistance genes and other useful traits harbored by the wild parents. Companion weed species also arose from such crosses, and these in turn influenced the evolution of the primitive crop varieties. Thus, periodic injection of genes from wild and weedy relatives increased the crop genetic diversity available to early agriculturalists for further selection and improvement, and enhanced the genetic capacity of the emerging crops to respond to changing environmental conditions. Indeed, today it is believed that many cultivated species might not have survived as domesticates without the genetic support supplied by their wild and weedy relatives. In addition to the diversity enhancing role of natural hybridizations, human migration and trade also played a major role in the crop evolution process. These activities occasionally brought together genetically dissimilar forms or races of crops, the crosses of which produced even more novel genetic combinations, thus further enhancing crop genetic diversity.

Gene flow between cultivated crops and their relatives, particularly in the gene centers, has occurred frequently in the past and still occurs today. Thus, the evolu-

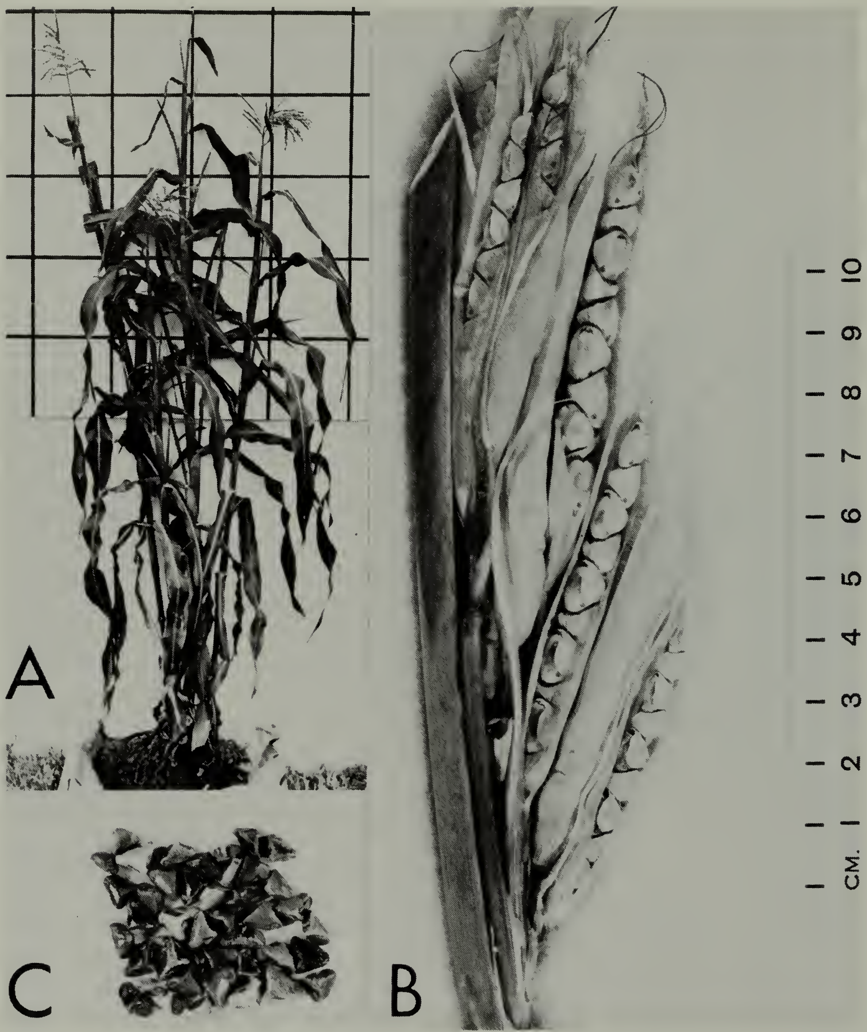


Fig. 4. Teosinte *(Zea/Euchlaena mexicana),* the closest wild relative of maize (corn). The morphological structure of teosinte (A) is very similar to that of maize. To the casual observer, the most reliable character which separates these two related species is the mature fruiting body; in teosinte, it is a doubly-segmented spike (B), while in maize it is a many-rowed structure (the familiar corn ear). Mature teosinte seed (C) is dispersed by the segments of the spike, which shatter easily. In contrast, the corn ear is non-shattering and thus retains its seeds after they mature. (Photo: With permission: H.G. Wilkes; *Economic Botany*)

tion of crop species continues in the remnants of the world's gene centers, wherever traditional forms of agriculture survive and primitive crops are allowed to coexist and interbreed with their wild or weedy relatives. Examples of such systems can be found in Mexico (Fig. 5), a gene center for maize (corn) and many other native American crops. Just as their prehistoric ancestors did, some traditional agricul-

turalists still skillfully manipulate teosinte, the closest wild or weedy relative of maize (Fig. 4), to increase their corn yields. Rather than eradicating these weedy plants from their maize fields, they allow them to remain within or near the cultivated crop populations (Fig. 5). When the wind pollinates the corn, some natural crosses occur. Although crosses such as these are not immediately evident, the following year when the new maize crop is planted from last year's seeds, the maize-teosinte seeds produce hybrid plants. In this way, the visible (phenotypic) effects of such accidental crosses can be observed (Fig. 6). Such maize-teosinte hybrids and their descendants are fully fertile and thus capable of passing on their genetic traits. Although allowing the weedy or wild relatives of crops to remain in cultivated fields may reduce yields in the short run, such "non-clean" cultivation practices have facilitated the accumulation of genetic diversity within populations of primitive crop varieties. As such, they constitute one of the most distinctive and important aspects of traditional agricultural practices. As an example, the great variety of primitive corn cultivars in the Mexican center of crop genetic diversity corresponds well with the heterogeneity of the social as well as the ecological environment. From the study of ancient farming methods and from archeological and botanical evidence (Fig. 7), we now understand that genetic interactions between maize and teosinte have played an important role in shaping the genetic constitution of this important seed crop (Fig. 8). Thus, although further research will be necessary to determine whether teosinte is in fact the wild progenitor of maize or merely a mutual descendant of corn's wild ancestor(s), it is evident that it has and is continuing to influence the evolution of corn.

Fig. 5. A Mexican hillside covered with harvested maize in fields separated by stone walls. The stone walls form rocky margins where wild teosinte is often found in abundance. (Photo: With permission: H.G. Wilkes; *Economic Botany*)

Fig. 6. A maize-teosinte hybrid *(Zea mays × Zea/Euchlaena mexicana)*. The result of a first generation cross (seed from a previous year's harvest), this plant is standing within a Mexican maize field at harvest time. The "cobs" are beginning to break apart, with the mature seeds being dispersed in pairs as two fused spikelets with four grains (seeds) each, instead of as individual seeds as in pure teosinte. (Photo: With permission: H.G. Wilkes; *Economic Botany*)

Fig. 7. The present and former distributions of teosinte populations in Mexico and Guatemala overlap those of primitive maize cultivars. Scrolls indicate locations where teosinte has been recovered among archeological remains. Hollow dots indicate populations known only from herbarium specimens. Solid dots represent extant teosinte populations. (Illustration: With permission: H.G. Wilkes; *Economic Botany*)

Similar processes could be detailed for wheat, potato, and other crop species. Considering the past and current importance of traditional agro-ecosystems in creating and maintaining useful crop gene resources, their rapid loss or transformation into seemingly more "productive" agricultural systems based on monocultures is a tragedy. Studies of technologically unsophisticated agro-ecosystems and of traditional farming practices have greatly facilitated our understanding of crop evolutionary processes. The loss of these systems has serious consequences for current plant breeding efforts. For plant breeders not only utilize the gene resources that they harbor, but they also employ knowledge of basic genetic interrelationships in order to determine which resources can be of the greatest use to us in crop improvement efforts. Information about the evolutionary histories of our major crops has reduced guesswork about plant relationships and thus the costs of crop improvement. Such knowledge facilitates the location and incorporation of resistance genes and other economically valuable traits for improving our modern cultivars.

Due to the tremendous value and importance of traditional agro-ecosystems, the National Academy of Sciences' (NAS) Committee on Germplasm Resources concluded that we should attempt to:

> Maintain areas of indigenous subsistence agriculture of the antecedents of major U.S. crops at their geographical sites of origin. This activity should be promoted in the immediate future, since areas of subsistence agriculture in lesser-developed countries are cur-

> rently diminishing markedly, due to increased industrialization, incursion of roads, replacement by modern techniques and high-yielding strains, and increase in large-scale monoculture (NAS, 1978, p. 98).

One important vehicle for conservation of such man-modified agricultural environments, together with the adjacent natural environments that contain wild relatives of crops, is the United Nations (UNESCO) Man and the Biosphere program's Project No. 8, "Conservation of Natural Areas and of the Genetic Material They Contain."

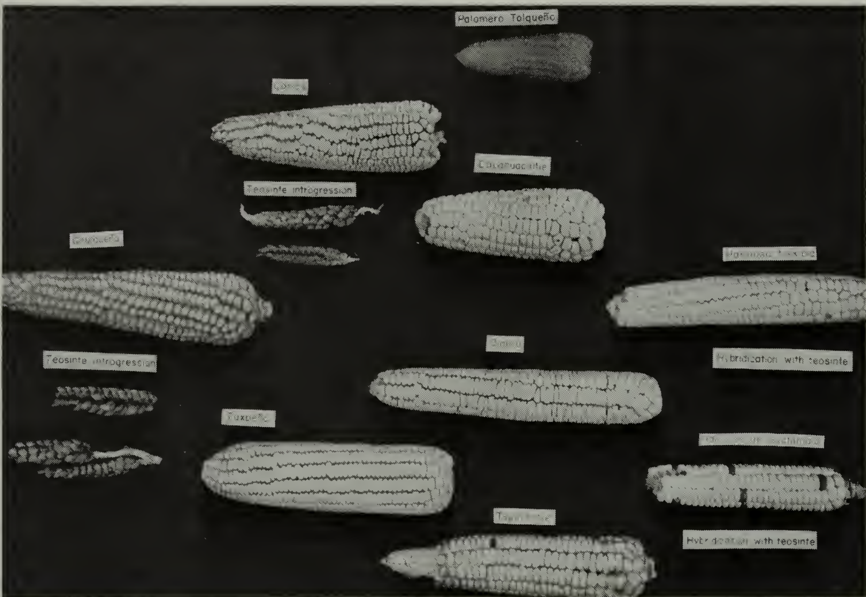


Fig. 8. The putative ancestry of Chalqueño—a primitive maize cultivar. Chalqueño is a very productive race of maize of relatively recent origin. It is the product of a cross between two other primitive maize varieties, Conico and Tuxpeño, and is believed to have also obtained part of its genetic make-up from Chalco teosinte with which it frequently shares the same fields. The postulated parents of both Conico and Tuxpeño are also shown, along with possible points at which teosinte influenced their evolutionary development. (Photo: With permission: H.G. Wilkes; *Economic Botany*)

Genetic Resources and Improvement of Major Crops

The sale of genetically improved crop varieties directly contributes more than $1 billion annually to the U.S. economy, and comparable amounts to the economies of other industrialized nations. The indirect contributions (increased wholesale and retail crop revenues) amount to many times this figure. Much of this productivity would not exist if it were not for the availability and use of wild, weedy, and primitive crop genetic resources and the crop gene centers from which they are derived. By far their most important contribution results from the location and use of genes for resistance to crop pests and pathogens. In the United States, on a percent of crop acreage basis, non-chemical means of crop pest control exceed chemical means (pesticides) for all major categories (insects, fungi, weeds). Crop genetic resistance is

one of our primary nonchemical options (others include biological and cultural controls). For example, disease-resistant crop varieties are currently grown on 75 percent of all U.S. croplands; and for small grains the figure is as high as 98 percent. Moreover, despite the estimated 1.9 billion kg/yr (4.1 billion lb/yr) of pesticides used worldwide, roughly half the annual world crop production is still lost to pests (both pre- and post-harvest losses). Losses due to disease pathogens alone recently topped $25 billion annually. Even though the United States must combat only a small fraction of the more than 10,000 insect species that currently attack world crops, insects still cause an estimated $5 billion damage each year in spite of the nearly 182 million kg/yr (400 million lb/yr) of insecticides sprayed on U.S. farmlands. Furthermore, U.S. crop losses due to insects have increased twofold since the 1940's, from about 7 percent to 13 percent, while use of insecticides to control these pests has soared tenfold. The failure of insecticides to control pests has been attributed to a variety of factors:

- increased planting of genetically susceptible crop varieties;
- reductions in crop diversity and the increase in monocultural practices;
- an increase in the number of pesticide-resistant pests;
- destruction of the natural enemies of crop pests by pesticides;
- reduced crop rotations, soil tillage, and sanitation;
- increased crop cultivation in marginal agricultural environments; and
- increased susceptibility of crop plants to pest attack due to physiological changes initiated by application of pesticides.

Clearly, crop resistance is one of our best devices for crop protection. Indeed, resistant cultivars are our only defense against many crop-specific parasites. Use of crop gene resources as sources of disease or pest resistance not only prevents or inhibits crop losses, but also lessens the need for costly, toxic pesticides. Although it has been estimated that pesticides return $3-5 for every $1 invested, their cost is steadily climbing because they are largely petrochemicals. While the returns from sale of agricultural produce to farmers have remained relatively static, insecticide costs have increased from $1.52/kg (69¢/lb) in 1970 to $4.03/kg ($1.83/lb) in 1977 (a 165% increase in about 7 years). By the year 2000, they might cost as much as $440/kg ($200/lb) as the cost of petroleum continues to rise. Moreover, pesticides often leave toxic chemical residues in soils and living tissues for long periods of time, and they have disastrous effects on nontarget species. For example, DDT was in large part responsible for the decline of the Brown Pelican and the Bald Eagle in the United States, while each year an estimated 200 deaths and 45,000 cases of accidental human poisoning in our country are attributed to pesticides. Worldwide more than 20,000 people die from contact with pesticides annually, and many others die later from cancer or suffer from delayed neurotoxic effects. In contrast, disease and pest resistance derived from natural sources offers a pest-specific solution to humanity's age-old problem of protecting its succulent and relatively defenseless crops.

Native crop production within gene centers has been observed to be lower than in areas to which crop species have been exported for cultivation. A major reason for this low productivity is that gene centers are also often centers of variability for coevolved or coadapted crop pests and diseases as well. Thus, introduction of crops to alien agricultural environments without their natural enemies has probably contributed more to crop productivity than any other factor. Within regions of crop

genetic diversity, the intensity of selection pressures by pests, diseases, and other environmental stresses forces crop populations to sacrifice some current productivity for the sake of future survival or adaptation. This in turn means that the option to cultivate native crops over introduced ones, and thus to rely primarily on native gene resources, must be balanced against productivity that will inevitably be lost due to the ravages of locally well-adapted indigenous pathogens and pests. So long as introduced crop species can be grown in the absence of their major natural enemies, they will enjoy a production advantage over affected crop populations. However, there is always the threat that some natural pest or pathogen of an important introduced crop will also become established (accidentally or intentionally) in the new (foreign) production area. The socioeconomic consequences of such introductions can be disastrous, as exemplified by recent efforts to combat coffee rust in Central America and to improve the genetic resistance levels of susceptible, but high-yielding *Hevea* rubber trees in the event of sabotage or accidental introduction of South American leaf blight to Asian producing regions.

There is certainly a lesson to be learned from this. One important observation is that if native crops are to be cultivated to any great extent, the conservation of what native wild and primitive gene resources are available is mandatory. A second point is that of the value and importance of international cooperation in the conservation and use of crop genetic resources. That is, what one nation has, others will invariably need; alternatively, other countries will be the primary suppliers of the crop genetic resources needed by the former nation. Hopefully, greater attention to this issue will enhance our awareness of the interdependency of all nations and peoples of the world. Finally, the ubiquitous nature of many plant predators and parasites, particularly rusts and other disease organisms that travel easily by wind and air currents, underscores the ultimate importance of conserving gene resources harbored within centers of crop genetic diversity. In the final analysis, it is these regions to which the world will turn first when a particular pest attains a broad or worldwide distribution.

At present, we simply do not know which agricultural genetic resources we will need most in the future. We have only just begun to really learn how to locate and use them extensively in crop improvement programs. Although much has been accomplished, we still have far to go—both in conserving gene resources and their habitats and in discovering new tools and techniques in order to use them more effectively. Therefore, as far as is humanly possible, we should keep our evolutionary options open for the present as well as the future.

Improvement of Crops Important in American Agriculture

The United States contains a minor crop gene center. Hence it offers useful germplasm resources for the improvement of only a few minor crops, including the sunflower (*Helianthus annuus*) and blueberry (*Vaccinium* spp.) (Fig. 9). Our role in providing essential gene resources to enhance world agricultural productivity has been relatively insignificant, although nationally and worldwide we can claim a few successes. For example, a wild blueberry from New Jersey has served as the source of canker-resistance for a commercial variety. This genetically improved blueberry replaced a susceptible cultivar in the southeastern United States. Similarly, the cultivated sunflower continues to benefit from incorporation of disease resistance genes and other useful traits obtained from wild American sunflower species. In recent

Fig. 9. Machine harvesting a native variety of blueberries in the northeastern United States. (Photo: USDA)

years, more than 0.4 million ha (1 million acres) of hybrid sunflowers have been cultivated in the United States, and about 0.6 million ha (1.5 million acres) in Spain. As an important oilseed crop, sunflower is now second only to soybeans in the United States, and it is first in the Soviet Union.

For the most part however, the reverse phenomenon prevails. As the following examples illustrate, American agriculture has profited tremendously from the extraction and use of agricultural genetic resources from foreign environments, particularly those from the less developed nations.

Potato *(Solanum tuberosum).* Ever since the experience of the Irish potato famine caused by potato late blight, wild species of potatoes and potato relatives have been instrumental in improving the resistance of our susceptible modern varieties. As J.R. Harlan has commented:

> One does not easily forget such experiences, and it is not surprising that wild species of tuberous *Solanum* are used routinely in breeding programs. For a time it looked as if the *R* genes from the Mexican *S. demissum* would solve the problem, but it turned out that the potato had only six *R* genes and *Phytophthora infestans* had nine or more, and other wild species had to be called in for service (Harlan, 1976d, p. 329).

Thus, genes derived from wild germplasm resources have supported modern potato varieties and have been used by potato breeders all over the world for decades. In addition to the late blight resistance genes donated by *S. demissum* (Figs. 10-11), this potato species and other wild solanums have yielded genes for immunity or resistance to frost, bacterial wilt, viruses A, X, and Y, races of golden and root knot nematodes, potato aphids, Colorado potato beetle, hopper burn, scab, leafroll, and

Fig. 10. For more than 40 years, blight-resistance genes from the wild *Solanum demissum* (right) have been used in modern potato cultivars such as 'Kennebec' (left). (Photo: Agricultural Research Service, USDA)

Fig. 11. The effects of potato late blight *(Phytophthora infestans)* on resistant (left) vs. susceptible (right) modern potato varieties. (Photo: USDA)

other potato disorders. Primitive potato cultivars, especially the *andigena* subspecies from the Andes of Peru and Bolivia, are known for their superior taste and culinary properties, and excellent tuber storage and seed viability properties; some types also possess substantially more nutritional value than modern potato cultivars. The socioeconomic potential of these primitive gene resources is vast, but to date they have been little utilized for their important genetic traits.

Tomato *(Lycopersicon esculentum).* The tomato is the most widely grown vegetable crop in the United States; in terms of total acreage, it is now second only to sweet corn. In recent years, the annual value of the U.S. tomato crop has topped $900 million. Much of this productivity hinges on the presence of effective resistance mechanisms to combat prevailing disease pathogens, particularly in California where tomato growers produce the bulk of the U.S. tomato crop. In 1977 California growers produced 76 percent of all commercial tomatoes sold in the United States and 86 percent of all tomatoes used for processing. Nearly all of the disease resistance genes which have been incorporated within modern U.S. tomato varieties were obtained from three or four introductions of the wild tomato species, *Lycopersicon pimpinellifolium* and *L. peruvianum,* from the South American gene center for tomatoes. For example, more than 100 of our advanced tomato cultivars carry a gene derived from the wild currant tomato (*L. pimpinellifolium)* (Fig. 12) which makes them resistant to *Fusarium* wilt. The 1947 release of the first wilt-resistant cultivar, 'Ohio W-R Globe,' saved the Ohio tomato industry alone more than $1 million annually. U.S. tomato growers still save millions each year from the use of modern varieties which owe their wilt-resistance to the single, dominant *I* gene obtained from

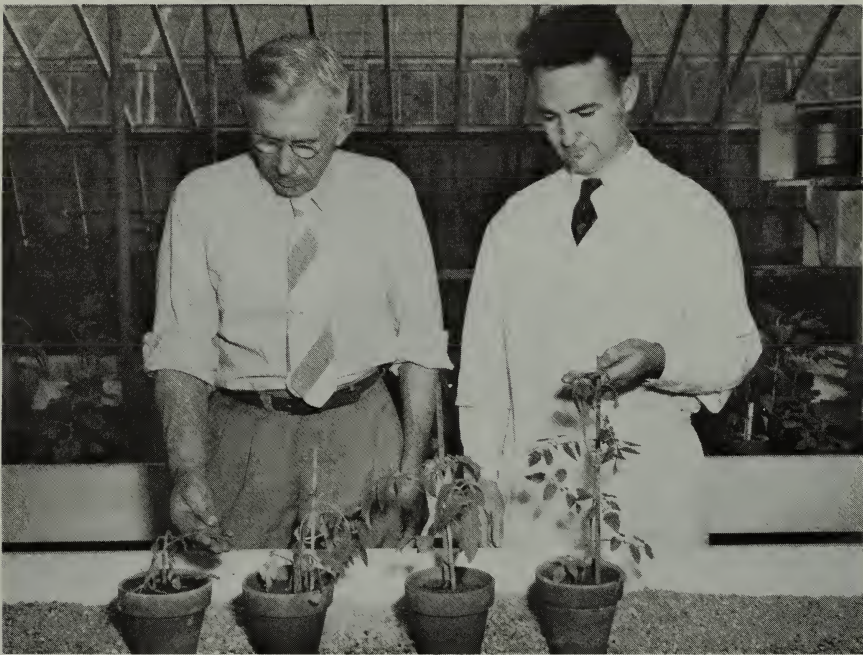


Fig. 12. The wild, small-fruited currant tomato *(Lycopersicon pimpinellifolium)* (far right) was the source of the gene that controls production of α-tomatine, an alkaloid that confers resistance to *Fusarium* wilt of tomato. The tomato plants on the left lack resistance to *Fusarium* wilt. (Photo: Agricultural Research Service, USDA)

this wild plant species. Genetic resistance factors are especially important to California tomato growers, since tomato cultivation there tends to be limited to advanced cultivars which have some degree of resistance to *Fusarium* and *Verticillium* disease pathogens. Ancestors of the currant tomato also played an important role in the evolution of cultivated tomatoes.

Other wild and primitive crop relatives of *L. esculentum* have offered increased vitamin C content as well as resistance to early and late blight, leaf mold, and gray leafspot. Others, such as the salt-tolerant *L. cheesmanii* of the Galapagos Islands, and the more distantly related, drought-tolerant *Solanum penelli,* may be particularly useful as sources of germplasm resources for the future improvement of modern tomato varieties.

Muskmelon and Cucumber (*Cucumis* spp.). Disease-resistant germplasm derived from wild melons has been extremely valuable to the cantaloupe industry. A wild species collected from the hills of India in 1937 later saved the California winter melon (*C. melo*) industry from the ravages of a new virulent race of powdery mildew. The savings amounted to approximately $5 million the first year. Moreover, many of our most important modern cultivars, such as 'Edisto' and 'Georgia 47,' owe their resistance to both downy and powdery mildew to this wild germplasm resource. More recently, a cross between the resistant 'Georgia 47' market variety and another wild melon has produced the hybrid 'Gulfcoast' which is resistant to gummy

stem blight. Losses due to this pathogen neared $500,000 each year prior to the release of this new cultivar. Furthermore, 'Gulfcoast' holds promise for significant expansion of the range of adaptation for this crop throughout the southeastern United States.

Primitive cucumber (*C. sativus*) varieties collected in India and Burma, the major center of genetic diversity for this crop, have similarly provided important sources of resistance genes to combat anthracnose and other cucumber diseases. However, the most important genetic trait—one that revolutionized the cucumber industry worldwide—is the gynoecious ("all female" flower) character obtained from the primitive Korean variety 'Shogoin.' In order to ensure the economic success of any mechanical harvesting process, a "once-over" harvesting operation is necessary. The gynoecious trait in combination with a trait which determines female flower clustering (rather than single flowers) were both discovered in 'Shogoin'; together these traits can facilitate mechanical harvesting. Prior to the use of this unusual gene resource, the high cost of producing hybrid seed by hand pollination severely limited the production and use of cucumber varieties in the United States. The first modern U.S. cultivar incorporating the "all female" trait derived from 'Shogoin' was released in Michigan in 1960. Today this hybrid pickling variety is the principal source of the gynoecious character now used worldwide for production of hybrid cucumber seed.

Sugarcane (*Saccharum* spp.). In the 1920's, a plant aphid which transmits a mosaic virus almost devastated the sugarcane industry in Louisiana. By 1926, production of refined sugar was down from 181,440 to 42,640 metric tons. Introduced mosaic-tolerant varieties from Java (now Indonesia), where the disease was endemic, saved the Louisiana cane industry from bankruptcy. These plant varieties were hybrids of Indian and Javan sugarcanes which derived their resistance from the wild cane *Saccharum spontaneum.* Wild sugarcanes have also conferred resistance to gummosis, red rot, and other disease pathogens.

Oats (*Avena* spp.). The use of the weedy oat, *Avena sterilis,* and wild oats (Fig. 13) for improving the genetic resistance of our cultivated oats (*A. sativa*) to crown rust (*Puccinia coronata* var. *avenae*), provide recent examples of additional crop productivity derived from extension of the ecological range of a crop as a result of greater control over disease. Oats is one of our major temperate-zone cereals. Now fourth in commercial importance, it enjoys a wider range of adaptation than either barley or wheat. Apparently this range expansion is continuing today through exploitation of the genetic diversity of wild or weedy oats such as *A. sterilis* from the arid regions surrounding the Mediterranean Sea. A total of 12 crown rust-resistant genes from *A. sterilis*, a progenitor and weedy companion of oats, have been recently incorporated in new multiline cultivars released during the mid-1970's. Recently, over one-fourth of the oats acreage in six southern coastal states was planted in these new multiline oats varieties. The 1976 farm-gate value of the crop planted on this additional acreage alone amounted to more than $12 million.*

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*The information which enabled the calculation of these benefits was assembled with the assistance of Dr. E. P. Imle, USDA International Programs Division, Dr. L. W. Briggle of the USDA National Program Staff, and Mr. Jim Naive of the USDA Commodity Economics Division, Economic Research Service.

Fig. 13. The Saia type of wild oats (left) was used as the source of genes for resistance to several rare races of crown rust *(Puccinia coronata* var. *avenae).* Resistance to the rust races was transferred from the wild oats to susceptible modern cultivars, such as the variety shown on the right, through the use of an intermediary oats variety—'Aberdeen 101' (center)—because the wild oats cannot be crossed directly with the cultivated varieties. (Photo: Agricultural Research Service, USDA)

Wheat (*Triticum aestivum*). The world's most widely grown cereal grain, wheat, has consistently benefited from genetic improvement efforts. The famous "Mexican" wheats—modern, high-yielding varieties (HYV) developed during the Green Revolution—were successful because their dwarf stature allowed the application of high levels of fertilizers without causing the plants to lodge or fall over. The dwarfing genes were derived from the primitive Japanese cultivar, 'Norin 10.' Wheat rust pathogens, such as stem rust *(Puccinia graminis tritici)* (Fig. 14) and stripe rust (*P. striiformis*), have caused a number of major epidemics in the United States. Each time a susceptible modern cultivar has succumbed to the ravages of such wheat-specific pathogens, resistant cultivars have been developed through the incorporation of resistance from conserved stocks of wheat gene resources. Nearly all of the rust-resistant sources of genes used in wheat improvement programs have been obtained from the crop gene centers where both wheat and its rust pathogens (*Puccinia* spp.) originated. Wild wheats from these areas, such as *T. timopheevii, T. comosum, T. speltoides,* and *T. umbellulatum,* have been used as sources of resistance to rusts as well as downy mildew, ergot, *Helminthosporium* blight and other diseases. For example, in the 1960's stripe rust finally reached epidemic proportions in areas of the Pacific Northwest. A wild or very primitive wheat from

Fig. 14. Wheat stem rust *(Puccinia graminis tritici)* attacking a susceptible wheat variety. This disease pathogen produces brick red, elongate pustules. (Photo: Agricultural Research Service, USDA)

Turkey (collected by Harlan in 1948) yielded the needed resistance. In recent years this gene resource has constituted one of the most important breeding lines used in Washington, Oregon, Idaho, and Montana. In Montana alone, annual losses due to stripe rust once approached almost 30 percent and totaled $2-3 million annually in many years. The primitive Turkish wheat also possesses resistance to over 50 races of disease-causing pathogens, including dwarf bunt which had resulted in another

$500,000 annual loss in western Montana. Nevertheless, upon initial evaluation as a potential gene resource, it appeared to be relatively useless to commercial producers. It is tall and has thin straw, and thus tends to lodge or topple easily. Moreover, it has poor milling qualities, lacks winter-hardiness, and is susceptible to leaf rust. Its subsequent evaluation and use for disease resistance in breeding programs for the Pacific Northwest demonstrates the value of maintaining crop germplasm resources even though their immediate commercial value may not be apparent.

In addition to their susceptibility to a variety of disease organisms, the cultivated wheats are also vulnerable to attack by more than 100 species of insects and mites. In the late 1960's, U.S. losses due to such pests were estimated at about $42 million annually. The Hessian fly (*Mayetiola destructor*) (Figs. 15-16) is one of the most injurious pests of wheat worldwide. It is believed to have been accidentally introduced to the U.S. via the straw beddings of Hessian soldiers during the American Revolution. Past epidemics of Hessian fly in the major U.S. wheat growing areas have been, in part, controlled by the development of resistant wheat varieties. By 1974, more than 28 resistant cultivars had been released for use in the United States, and Hessian fly-resistant wheats were being grown on approximately 6.5 million ha (16 million acres). At least one resistance gene used in the development of these varieties was obtained from a primitive wheat from Portugal, which a U.S. plant explorer collected in 1930. In 1969 when resistant wheats were grown on more than 40 percent of the 8 million ha (20 million acres) infested with Hessian fly, farmers saved an estimated $17 million. The total cost of the development of all U.S. varieties resistant to this pest has been estimated at only $6 million. Thus, only 1 year's savings offset the costs of developing all of the Hessian fly-resistant wheat varieties used during the last half century.

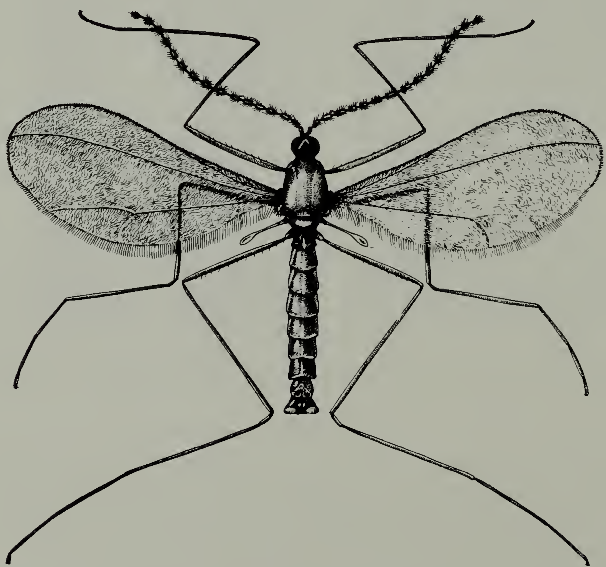


Fig. 15. An adult male Hessian fly (greatly enlarged). (Illustration: Agricultural Research Service. USDA)

Fig. 16. An adult Hessian fly perched on a wheat seedling during a 1976 study to determine the genetics of Hessian fly virulence. This study facilitated the development of new Hessian fly-resistant wheat cultivars. (Photo: Agricultural Research Service, USDA)

Asian rice (*Oryza sativa*). Another important cereal crop, Asian rice, has been much improved through the incorporation of genes derived from wild or primitive germplasm resources. For example just as in the case of the high-yielding dwarf wheats, the development of the high-yielding dwarf rice varieties led to enormous increases in world rice productivity. The single recessive gene for semidwarfism was donated by the primitive Taiwanese cultivar 'Dee-geo-woo-gen.' Other primitive cultivars have been employed to enhance the usefulness of the modern Green Revolution rice varieties through improvement of their genetic capabilities to tolerate drought and deep-water. Some primitive varieties from southern India and Sri Lanka have conferred resistance to different genetic strains of brown planthoppers in the Philippines. Although many genetically diverse, primitive varieties are relatively unaffected by plant or leafhopper species, various high-yielding IRRI*—HYV rice cultivars, such as 'IR-8,' have suffered from repeated outbreaks. In addition to directly affecting crop production, these insects often carry a virus disease which also attacks 'IR-8'. Resistance to grassy stunt virus *per se* has recently been incorporated into eight new IRRI rice varieties. *Oryza nivara,* the wild donor species, is currently the only known source of natural resistance to this devastating rice virus.

These examples of the utilization of wild, weedy, and primitive germplasm resources give some indication of the economic value of the gene pool resources from which they were obtained. Many more could be cited, and as new techniques for locating and transferring specific genetic traits are developed, the use of naturally occurring sources of genetic variability will increase.

*International Rice Research Institute

Although in the past, plant breeders relied almost exclusively on improved varieties in their search for useful gene resources, in recent times resistance genes have frequently been obtained by crossing commercial cultivars with their unimproved wild or weedy relatives. When using standard plant breeding techniques, however, some of the more economically desirable traits of the advanced cultivars are often lost during crossbreeding. Alternatively, subsequent breeding and selection to achieve an economically more useful product often results in dilution of the desired genetic resistance factors to a level of insignificance.

The development of new tools and techniques which facilitate the location, evaluation and actual use of desirable gene products from primitive cultivars and wild and weedy stocks is currently remedying some of these problems. One established technique used to overcome hybrid sterility barriers which arise during crosses between related species with different numbers of chromosome sets is that of using colchicine (from the autumn crocus) to induce needed changes in the number of chromosome sets present in different breeding materials. A relatively new tool, electrophoresis, can be employed to some degree for screening or evaluating the proteins (gene products) present in different crop genetic materials. Electrophoresis also allows us to better study the existence and maintenance of genetic diversity in crop (and livestock) populations. And for some crops, use of alien-addition lines to create alien-substitution lines which allow the transfer of genes from distant wild relatives of crops has become a standard breeding practice.

Future technological innovations and further advances in the study of plant evolution, taxonomy, and genetics will open new doors to the use of unimproved crop genetic resources. Our current situation and prospects for the future use of wild gene resources have been summarized as follows:

> The current trend toward genetic uniformity and the loss of the old "land" cultivars in many crops is resulting in the erosion of genetic variability. Furthermore, in a number of crops the known genes for disease resistance are being used up as they are released in cultivars and then overcome by new races of a pathogen. Thus it is likely that wild species will become increasingly important sources of germplasm in the breeding of many crops....
>
> At present, genes can be transferred only between related species although further development of techniques such as somatic cell hybridization, transduction, and DNA transformation may change the picture in the future. Many procedures can be used in making gene transfers and the one that is appropriate for a particular situation depends on the relationship between the two species involved (Knott and Dvořák, 1972, pp. 211-212).

Improvement of Crops Important in World Trade

In addition to the direct benefits of crop improvement to the U.S. economy *per se,* many of the cash crops currently important in world trade, such as cacao—the source of chocolate and cocoa (Fig. 17)—have been supported by wild or primitive genetic resources:

> The terror of famine has stalked man since the beginnings of agriculture, but one may be hurt almost as badly if the money crop fails. This has happened to countries economically dependent on sugar, cacao, coffee, tobacco, and bananas. Mosaic virus has brought the sugarcane industry to the brink of disaster in several areas. The problem was first solved in Java by introducing resistance from wild *Saccharum spontaneum*.... Wild sources of cacao have saved the industry from devastating witches broom, and wild cof-

fees are resistent to rust, *Hemileia vastatrix.* Coffee rust has essentially wiped out the arabica industry in Ceylon, India, Java, Malaya, the Phillippines, and a dozen countries in Africa. Tobacco-dependent economies have been salvaged by transfer of mosaic immunity from *Nicotiana glutionosa* in 1938 and wildfire immunity from *N. longiflora* in 1947 (Harlan, 1976c, pp. 329-330).

Today approximately 30 races of coffee leaf rust still threaten the coffee industry and the billions of genetically susceptible coffee trees in the western hemisphere. Even though coffee originated in Africa, some 80 percent of the world's coffee comes from the cultivated species *Coffea arabica* (Fig. 18) which today is grown mostly in Central and South America, especially Brazil. The importance of coffee to the western producing nations has been amply expressed by members of the USDA Coffee Rust Team recently dispatched to Central America:

> In dollar value, *coffee is the second most important commodity in international trade,* petroleum being first. In some parts of the world, coffee is the only source of income for millions of people. It is produced in more than 40 countries, 16 of them in the western hemisphere...An estimated 700,000 farmers engage in coffee production. Millions more people make their livelihood from picking, handling, shipping, processing, and selling coffee (Imle et al., 1977, p. 2).

Fig. 17. A cocoa pod from cacao *(Theobroma cacao).* Dried, fermented cocoa beans are exported worldwide, primarily from Latin America and Africa. Currently a prime objective of cacao improvement programs is the location of wild germplasm resources which confer resistance to the many insects and diseases that attack this important crop. (Photo: USDA)

Fig. 18. Today nearly all *arabica* coffee is obtained from high-yielding, but genetically uniform coffee trees selected from parental stock involved in only two separate New World introductions. The 'Bourbon' variety, depicted here, was initially introduced to the Caribbean by the French and was later transported to South America. (Photo: Agricultural Research Service, USDA)

Coffee leaf rust (*Hemileia vastatrix)* appeared first in Ceylon (now Sri Lanka) in 1869, and gradually invaded the rest of the *arabica*-producing regions of the eastern hemisphere. Suddenly, in 1970, coffee rust was discovered in the western hemisphere in southern Brazil. Brazilian coffee production suffered even though the flat terrain and monocultural cultivation practices allowed growers to combat the fungus with costly copper-containing fungicides. In November 1976 the rust appeared in Nicaragua, and a wave of alarm spread throughout Central America and beyond. Uncontrolled rust infections can kill or weaken coffee trees within a few years. Unchecked, it could reduce Central American production by more than half. In 1976-1977, Central America exported almost a half billion kg (1 billion lb) of coffee, and 1977-1978 exports were expected to bring an estimated $2.5-3 billion to these developing nations. With so much at stake, economic pressure has increased to do almost anything to prevent or delay the spread of the rust epidemic. Yet, completely

eradicating 14,170 ha (35,000 acres) of trees in the infested areas was considered as unacceptable as letting the disease spread unchecked. Moreover, ultimate success could not be guaranteed anyway. Indeed, the strategy of eradication had already failed in Brazil. Furthermore, it would have caused severe political and social upheaval and would have cost about $50 million.

Nicaraguan officials decided on limited eradication, and sought advice for both short- and long-term measures. In response, the U.S. Department of Agriculture and the U.S. Agency for International Development dispatched the Coffee Rust Team early in 1977. The team found that spray control programs would not be nearly so effective in Nicaragua as they had been in Brazil. In Nicaragua the dense trees and steep mountains inhibited the use of spray equipment. Furthermore, safe and effective, but inexpensive fungicides were not available. Before the onset of the rainy season and the new rust infections it would bring, Nicaragua had expended nearly $6 million on control programs, and set in motion the authorization for another $10 million. Although limited control may help temporarily, most growers must upgrade their production technology or abandon coffee production entirely. The Coffee Rust Team concluded that:

> The best control for coffee rust will be to develop good commercial varieties with rust resistance....
>
> If a properly coordinated and adequately funded network for international cooperation is developed, it is certain that within a few years seeds of adapted, high-yielding, rust-resistant varieties can be produced by each country in sufficient quantity to support massive replacement of susceptible trees with resistant ones.... With costs of spraying estimated at $200 per hectare, the cost-benefit ratio for development of rust-resistant plants, which will require little or no spraying, is very great. Investments in a proper program to produce resistant plants will pay huge dividends. Additional dividends will come from discovery of resistance to nematodes and to some of the other coffee diseases which are not now being controlled (Imle et al., 1977, pp. 11-12).

Fortunately, fearing the occurrence of such an epidemic and knowing that modern *arabica* coffee cultivars are susceptible to coffee rust, officials and researchers located sources of disease-resistant germplasm 20 years ago. Cultures of the 30 races of the *Hemileia* pathogen were preserved for extensive use in a plant screening program eventually established in Portugal. In 1964-1965, a group of plant explorers was sent to the tropical Ethiopian highland forests, the center of *arabica* coffee genetic diversity and the traditional source of coffee germplasm resources. They arrived just in time. More than seven-eighths of the original Ethiopian forest, of which wild coffee trees are a part, had been removed and new roads were cutting into the remainder. The collection of remaining wild coffee gene resources from the remnants of this tropical forest has been recently classified as urgent.

As a result of these efforts future progress appears promising. A coffee germplasm collection containing over 4,000 accessions now resides in Costa Rica. Many of the selections there are known to possess genes for resistance to the coffee rust fungus. A hybrid between the preferred *arabica* type and the less economically desirable but more resistant Robusta coffee species, *C. canephora,* resists all 30 races of coffee rust (*Hemileia*). This invaluable hybrid is now being used as parent material in further *arabica* crosses. In Brazil, its progeny are being selected for better quality (flavor), disease resistance, and yield. Some resistant hybrids are already being used for emergency plantings. In addition, a naturalized, wild-type coffee was discovered on the Island of Timor, where there are no indigenous wild coffees. The island peo-

ple began to cultivate it in the 1940's, and since it is assumed to be a *C. arabica* x *canephora* hybrid, it has become known as the "Híbrido de Timor." The progeny of this natural hybrid are generally resistant to group A races of coffee leaf rust, and since they have the same chromosome number as *C. arabica,* they will cross readily with the economically preferred coffee species. It has already been widely used for breeding rust-resistant *arabica* coffee cultivars in Costa Rica, Brazil, and Colombia, as well as in Tanzania, India, and Portugal.

New Crops

A number of "new" world crops promise to enhance the quality of life in tropical and developing nations and to provide some novel foods for consumers in industrialized nations as well. In addition to their sociocultural value, new crop introductions can have profound economic consequences. Consider, for example, the introduction of soybeans (*Glycine max)* into the United States as a new crop in 1930. This ancient Chinese crop plant is currently the world's most important "grain" legume species, and today the United States leads in world soybean production (74 percent in 1973). In the early 1930's, the cost of the soybean explorations amounted to $30,000. Even though this was a great sum of money at that time, the revenues returned to the U.S. government in the form of taxes paid by soybean farmers since then have more than paid for the entire cost of all U.S. crop explorations from 1898 to the present. And the soybean is only one of many "new" crops introduced into the United States since the turn of the century!

Although some new crops such as triticale (a cross between wheat and rye) are innovations of modern science, as the soybean example demonstrates, most of our novel crops are not really new at all. Most have been cultivated instead as a primitive crop species or harvested as a wild food resource by other peoples since earliest times. Thus, in many instances we have only discovered the existence of exotic, minor crop species. Exotic fruits (or their products) which frequently appear in U.S. markets, yet which are commonly cultivated in other countries, include guava, passionfruit, kiwi, mango, papaya, pineapple, tomatillo, "tuna" (*Opuntia* cactus fruit), Macadamia nuts, litchi nuts, palm nuts, kumquat, and loquat. In other instances, we have merely rediscovered wild foods or very ancient crop cultivars which have fallen into disuse. For example, a multitude of minor leguminous crops and wild legumes cultivated or collected by certain tropical or subtropical peoples are now being investigated as potential new, nitrogen-fixing crops for harsh tropical environments and marginal arid lands. Examples include the yam bean, marama bean, bambara groundnut, jackbean and swordbean, winged bean, tropical lima bean, tepary bean, tamarind, and tarwi—a disappearing minor crop. Additionally, some minor crops and wild species which are better adapted to cooler temperate climates are also being rediscovered and genetically improved. Two such plants that were once staple foods of native American Indians, Indian wild-rice and amaranth, are now being enjoyed by many American families.

Domestication of Indian Wild-rice

Thomas Jefferson once wrote, "The greatest service which can be rendered any country is to add an useful plant to its culture; especially a bread-grain." Today, approximately 150 years later, the combined efforts of some Americans are bringing

one of our only native cereal grains into domestication. Indian (northern) wild-rice (*Zizania palustris*) has been harvested from natural stands in the Great Lakes and northeastern regions of the United States by various Indian tribes for centuries. In recent years, both native Chippewas and other Americans have scrambled through wild stands in the northern lake country of Minnesota, harvesting the grain for personal consumption and sale. Although the historical and potential economic value of wild-rice has been known for some time, only recently has it assumed economic importance as a very expensive cereal grain ($14.10/kg or $6.40/lb in 1976). In 1976, 0.7 million kg (1.5 million lb) of the processed grain harvested from 3,600 ha (9,000 acres) produced an income of $5 million for Minnesota growers. As the area in production increases, the cost of this nutritious cereal crop will likely fall more within the budget of most American consumers. Indeed by 1981, 0.91 million kg (2 million lb) of grain grown on 6,700 ha (15,000 acres) brought wild-rice growers $8 million; the processed grain sold at an average retail price of $11/kg ($5/lb).

Genetic improvement and expanded production of this new crop seems warranted. Unimproved wild-rice contains more protein and lysine than the average available in most commercially cultivated types of rice, corn, rye, barley, sorghum, and white or soft wheats. The lysine content of the much touted 'Opaque 2' corn and 'Hi-proly' barley cultivars does not yet match the average amount found in wild-rice. The protein content of most commercial cultivars of rice (*Oryza* spp.) is about half that of wild-rice. Moreover, the average amount of protein in the latter is about the same as the highest values for Asian rice. Wild-rice compares favorably with oats, the cereal considered to have the highest amounts of lysine and protein, besides containing higher percentages of some basic amino acids than either oat groats or hard red wheat. The prospects for this unimproved wild species look very good, as wild-rice breeder E. A. Oelke has observed:

> . . . we feel wild rice has an excellent chance of being our next domesticated cereal grain. Man will be able to use many northern, low wetlands for growing a crop, thus adding considerably to our food supply. The potential in Minnesota alone is 100,000 acres or more (pers. comm.).

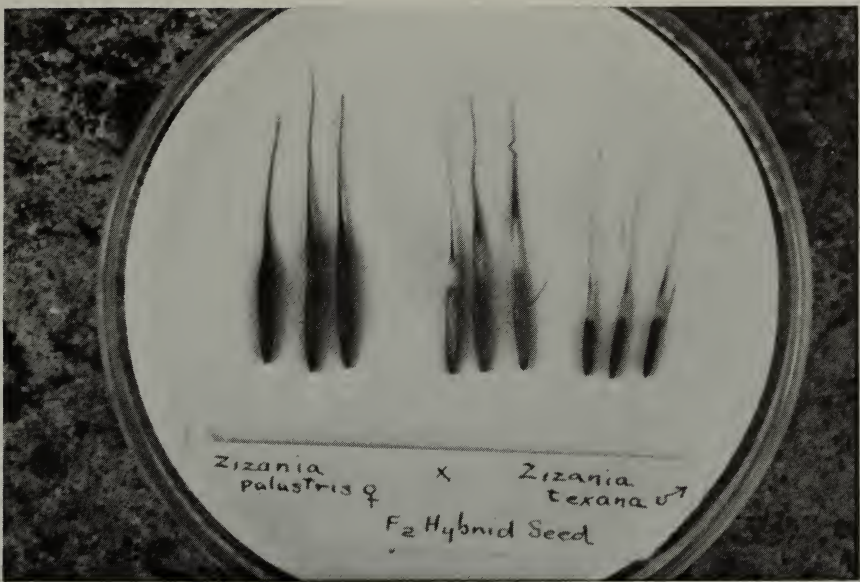
Commercial cultivation of wild-rice was suggested as early as 1852, yet no serious attempts were made until 1960. The most crucial step in the domestication of any wild grain plant is the location of "nonshattering" genetic resources, i.e., sources of genes that prevent or reduce the release of the grain or seed upon maturity. In the wild, shattering plants have an adaptive advantage because they leave more offspring by releasing mature seeds to the soil. However, the reverse is true for plants adopted for cultivation, since the seed grain must be retained by the parent plant so that it can be harvested by man. In 1963 the first nonshattering wild-rice was located. Seed samples obtained from this genetic type were eventually tested in 1967 with mechanical harvesters such as those used in southern rice production. Whereas good yields of shattering wild-rice produced only 91kg (200 lb) of unprocessed grain and required up to six or seven passes through the field, a single harvesting operation with the selected wild strain yielded 318 kg (700 lb) of grain on the test plot. Since these new advances, wild-rice production in Minnesota has increased from a few hundred to some 5,260 ha (13,000 acres) by the mid-1970's. Moreover, genetic improvement of this new crop, particularly for resistance to insect pests and diseases such as *Helminthosporium* blight, promises to expand present production potential significantly and further facilitate mechanical sowing and harvesting.

As is true for the major crop species, genetic improvement of this wild food plant requires the assemblage and exploitation of gene pool resources. One closely related, native American species is Texas wild-rice (*Zizania texana*), an endangered, perennial species. Crosses between this endangered relict and the presently cultivated *Z. palustris* have been made (Figs. 19-20). Most of these are fertile and could be utilized in breeding improvement programs. In time, Texas wild-rice may provide useful genes for disease resistance and other adaptive traits. Both the seeds (grain) and foliage of this rare plant are exceptionally nutritious.

Unfortunately Texas wild-rice was nearing extinction when its value as a potential gene resource was finally acknowledged. By that time, much of the genetic diversity once available had already been irretrievably lost. At present the species is restricted to part of a riverbed habitat within the city limits of San Marcos, Texas. During the last half century, it has suffered a tremendous decline. In earlier years, cattle were frequently observed grazing on it, walking into the river and submerging their heads deep into the water. Wild-rice plants along the river banks were gradually eliminated. Where it was formerly very abundant in the upper reaches of the San Marcos River, it has been virtually eliminated by streambed plowing, cutting, and vegetation removal for city park and lake maintenance. Spring lake mowing activities at a local tourist attraction regularly released masses of aquatic vegetation which floated downstream and damaged or destroyed emergent flowering or fruiting heads. Commercial aquatic plant collectors have often pulled up wild-rice and other plants that were not suited for aquaria, and sometimes replaced them with exotic or other saleable species; private collectors and aquaria enthusiasts have also taken a toll. Pollution from raw sewage leaks and the city storm drainage and watershed runoff systems have had a detrimental effect on the remaining population. By 1977 the remaining individuals had not been observed to reproduce, either vegetatively or sexually, for at least 10 years. Furthermore, attempts to reintroduce plants to former habitats have been relatively unsuccessful. The artificially established plants have suffered from the depredations of an introduced mammalian pest, the nutria (*Myocastor coypus*), as well as other factors which contributed to the decline of the original populations.

Presently, the greatest obstacles to further research on the breeding potential of Texas wild-rice are its continuing decline, loss of habitat, and lack of funds to support needed research. These problems should be remedied so that this endangered species will be available to meet future germplasm needs for the domestication and genetic improvement of Indian wild-rice. Conservation of intact, undisturbed habitat would be the best means to preserve the species. And preservation of this endangered species is warranted. In the words of Dr. E. A. Oelke, who is centrally involved in current efforts to domesticate Indian wild-rice:

> . . . it is essential that we preserve all available germplasm of *Zizania* species for future use in the development of varieties which are more suitable for cultivation and more widely adapted, so this nutritious grain can be produced in many more northern areas of the United States and the world (pers. comm.).



Figs. 19 and 20. A wild-rice hybrid grain *(Zizania palustris × texana)*, Progeny of crosses between Indian or northern wild-rice and the endangered Texas wild-rice are currently being selected for such useful characteristics as increased yield, disease resistance, and a non-shattering habit. Since Texas wild-rice is now close to extinction, hybridization with more common wild-rice species may ultimately prove to be our only means for perpetuating the genes harbored within this endangered but economically important species. (Photos: W.H.P. Emery, Southwest Texas State University)

The Genetic Improvement of Amaranth

Another forgotten food of the ancient Americas that deserves special attention is amaranth (*Amaranthus* spp.). Approximately 60 native wild and weedy species exist in the New World. From these, native American Indians domesticated the first primitive cultivars. Three separate domesticates arose and were widely cultivated throughout North, South, and Central America before the arrival of the Spanish conquistadors who later suppressed the culture of amaranth. This historical course of events has been summarized as follows:

> Five hundred years ago, amaranth grain was a staple of the Aztec diet and an integral part of their religious rites. The Aztecs made idols out of a paste, composed of ground, toasted amaranth seeds mixed with the blood of the human sacrifice victims. During the religious festivals, the idols were broken into pieces that were consumed by the faithful, a practice that the Spanish conquistadors considered a perverse parody of the Catholic Eucharist. When the Spaniards subjugated the Aztecs in 1519, they banned the Aztec religion and with it the cultivation of amaranth....(Marx, 1977, p. 40).

Thus, maize, beans, peppers, tomato, squash and other cucurbits were acquired for cultivation by Europeans colonizing the New World, but amaranth was left behind. Today, it is grown commercially in only a few places in Mexico, where the peasants use the grain (seeds) to make candy and other confections. On the other hand, it was introduced relatively recently to the Old World, and has been cultivated as a seed and vegetable crop, particularly in India, for at least a century. That was the status of this native American crop until a few years ago, when work on the use and improvement of *Amaranthus* cultivars was initiated at the Rodale Organic Gardening and Farming Research Center in Pennsylvania (Fig. 21).

Today, after hundreds of years of widespread neglect this photosynthetically efficient, drought-resistant plant finally is being investigated for its nutritional value, culture, and marketing feasibility. Amaranth is an excellent source of high-protein, high-lysine seeds and foliage. The seed ''grain'' yields a high quality, easily digestible protein which, due to its nutritious amino acid balance, is very similar to soybeans. Since it is rich in the essential amino acids that are lacking in corn, wheat, and rice, i.e., lysine and the sulfur-containing amino acids, amaranth flour complements cereal flours well. Yet, unlike soy flour, amaranth flour has exceptional baking qualities. It is very mild tasting and, like wheat, forms gluten so that bread and muffins will not crumble. One species of amaranth has been proposed for special use as a livestock forage plant. Moreover, both wild and cultivated species are valuable sources of leaf protein for the production of food concentrates for animal and human consumption. As the genetic improvement of this ancient crop continues, more Americans will probably consume nutritious amaranth seeds and leaves.

As archaeologists and historians continue to unravel the secrets of early cultivators and their ancient crops, and plant breeders continue to domesticate new crop plants from wild species, more novel foods will be found in the American market. This process of food diversification is one means of decreasing our dependence on the handful of genetically vulnerable major crops to which our future is presently tied.

Fig. 21. Grain amaranth plants growing at the Rodale Experimental Farm in Pennsylvania. In addition to conducting cultivation trails, researchers at the Rodale Organic Gardening and Farming Research Center have assembled an important *Amaranthus* germplasm collection and have been selecting for improved vegetable and "grain" (seed) amaranth strains. (Photo: Rodale Press Inc.)

3

Animal Resources and Food Production

Just as in the case of our food plant species, both wild and domesticated animal species contribute directly to agricultural productivity; they provide meat, fish, milk, eggs, animal fats and oils, and honey. Between 1950 and 1960, total world meat output, primarily from domesticated animals, amounted to $40 billion with roughly 7 percent—or $3 billion worth—of this production entering world trade. Currently meat from wild animals or "bushmeat" provides less than 1 percent of total world meat production. However since the mid-1960's, world output of bushmeat has practically trebled, and the estimated value of 1978 exports (about 7 percent of that year's total productivity) was $140 million. Fish and shellfish, however, provide the most significant direct contribution of wild species as food. In 1965, the world catch (at the fishermen's level) for marine and inland waters totalled 52 million metric tons, and was valued at $7-8 billion. International trade in fisheries products in that year amounted to $2 billion and constituted about 7 percent of trade in all primary agricultural products. Moreover, in recent years annual production derived from wild species of fish and shellfish has varied from 65 to 75 million metric tons. Although annual harvests from marine waters have been substantial, indications are that some fisheries are being overharvested. To the extent that this is true, present harvesting policies will have a detrimental effect on the total long-term productivity of these fisheries.

In addition to their direct use as food, wild and domesticated animal species serve mankind indirectly in the food production process as: crop pollinators which service populations of both cultivated crops and wild crop gene resources, biological control agents, draft or hunting animals, and sources of fertilizers. The value of U.S. crops dependent on insect-pollination in 1967 was estimated at $1 billion; an additional $6 billion worth of crops benefited from bee pollination. These crops supply roughly one-third of the American diet. Without the services of insect pollinators, we would probably lose at least $4 billion annually, and would have to rely on self- and wind-pollinated crops almost entirely! Moreover, an absence or depletion of

pollinators, e.g., through exposure to pesticides, can be devastating for farmers who depend on insect-pollinated crops, e.g., blueberries, apples, and alfalfa (Fig. 1). Many crop plants are pollinated primarily by "generalist" pollinators that service many species, such as the domesticated honey bee (*Apis mellifera*). In contrast, "specialized" pollinators, e.g., the fig wasps of the family Agaonidae, have each coevolved with the specific plant species they pollinate. Thus, each fig (*Ficus*) species can be pollinated only by its specialist wasp pollinator, and fig plants introduced into new areas for cultivation without their pollinators will not bear fruit.

Using wild insect species as biological control agents has actually saved some agricultural industries in the United States from economic extinction, and has increased agricultural productivity through control or destruction of introduced crop

Fig. 1. A pollen-laden honey bee *(Apis mellifera)* pollinating an alfalfa *(Medicago sativa)* floret. The multi-billion dollar alfalfa hay crop is grown annually from seed produced entirely by bee pollination. Introduced honey bees are often used to pollinate alfalfa since they also utilize the nectar for honey production. However, wild bees, such as the native alkali bee *(Nomia melanderi)* of the western U.S. and the alfalfa leafcutter bee *(Megachile pacifica)* introduced from the Old World, are much more effective pollinators of alfalfa. (Photo: Agricultural Research Service, USDA)

pests. Ladybird beetles (Fig. 2) have proved especially valuable for control of aphids, scale, and other destructive insect pests. An excellent example is that of the control of cottony-cushion scale of citrus (*Icerya purchasi*). This exotic scale insect was accidentally introduced around 1868 to Menlo Park in northern California on an ornamental *Acacia* tree from Australia. By 1886 the scale insect was devastating the growing citrus industry of southern California; citrus trees were so badly damaged that they had to be pulled and burned. Real estate values began to plummet. In the spring of 1889 shipments of live ladybird beetles (*Vedalia cardinalis*) from Australia were liberated in citrus growing areas, and by 1890 the scale infestation had been brought under control. The total cost of the project amounted to around $5,000, yet the benefits to citrus growers have amounted to millions of dollars each year thereafter. Then, in 1946-1947, DDT sprayed in these California citrus groves virtually destroyed the ladybird beetle populations and resulted in a new population explosion of the scale insects. Growers offered to pay $1 for each live *Vedalia* beetle which were rapidly collected from other locations in southern California, and they modified the DDT spraying program so that biological control of the destructive scale insect could be maintained by the reestablished ladybird beetle population.

Some wild species have been domesticated by man to hunt other animals or to provide draft power. Cheetahs, ospreys, hawks and falcons, and even seadiving cormorants were once domesticated or tamed and used to track or catch other food animals; some are still used for these purposes. Certain breeds of cattle and horses, the donkey, water buffalo, camel and dromedary, llama, reindeer, elephant, and yak have all served as draft animals. In a few instances closely related species have been

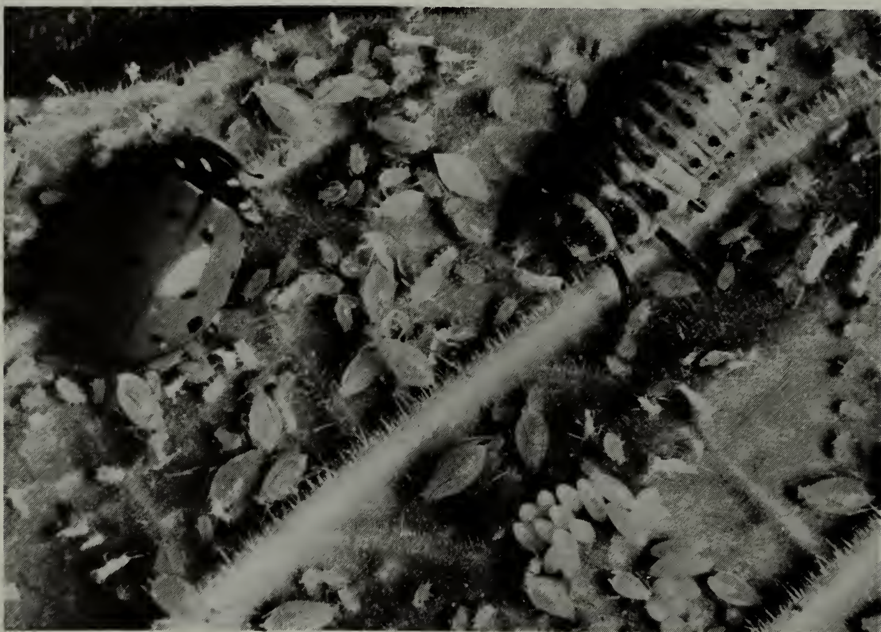


Fig. 2. An adult ladybird beetle and larva feeding on aphids. (Photo: Clemson Agricultural College, South Carolina)

crossbred to yield superior draft animals. The farm mule is a cross between a mare (*Equus caballus*) and donkey (*Equus asinus*), and the yakow is a cross between zebu cattle (*Bos indicus*) and the domesticated yak (*Bos grunniens*). Where motorized vehicles are either too expensive to buy and maintain or are inappropriate for the prevailing terrain, animal traction will probably remain the predominant form of power for cultivating, harvesting, and transporting agricultural produce (Fig. 3). Some animal species are used to drive milking, threshing, and irrigation equipment as well; and a few species, e.g., cattle, water buffalo, and camels, are prized as multiple purpose animals that provide draft power as well as meat, milk, and cheese. Animals, especially in developing countries, are also used frequently as a source of much needed manure for fertilizing crop plants. However, from the perspective of world trade, seabirds such as gannets and cormorants provide the most important commercial sources of natural fertilizers. Through conservation and management of seabird populations and their prey, Peruvian seabird guano production increased tenfold between 1900 and 1971, from 20,000 tons to over 200,000 tons annually. On islands off the south and southwestern coasts of Africa, breeding colonies of gannets have yielded an average of nearly 4,000 tons from 1961-1972. In 1969 the guano from these seabirds sold for about $7.10 for a 91-kg (200-lb) bag and was worth twice the economic value of the fish they consumed to produce it.

Stone Age man obtained virtually all animal foods from wild species such as buffalo, deer, reindeer, birds, fish, molluscs, and crustaceans as well as from aurochs (wild cattle) and other wild ancestors of our domesticated animals. Yet despite the plethora of wild food species available, today only the few remaining

Fig. 3. A Thai farmer watching his son learn to plow a rice paddy with the aid of a water buffalo. (Photo: USDA)

tribes of hunter-gatherers, some recreational game hunters, and pastoral peoples still regularly use or depend on wild animals for food. Most people now obtain the bulk of their animal protein and calories from a handful of genetically improved, and more productive species which were acquired over thousands of years of domestication. Thus, today we have domesticated cattle, sheep, goats, chickens, turkeys, ducks, geese, pigs, camels, reindeer, and water buffalo; and semidomesticated oysters, catfish, musk oxen, antelope, and deer. And we are now considering a few other wild bushmeat species for game ranching or domestication. Unfortunately, during the course of the lengthy domestication process, many of the wild progenitors (ancient ancestors) and other close relatives of our favorite domesticates have been hunted or harvested to the point of extinction, or they have been nearly replaced ecologically by their genetically improved progeny (Table 1; see also Figs. 11-13). One such example is the extinct aurochs (*Bos primigenius*) which once thrived in Europe and is believed to be the wild progenitor of most modern-day cattle breeds. In addition to the gene resources of our domesticates, there are many other extinct or endangered wild species that could have been used in a semidomesticated state had we had the interest or foresight to adequately conserve their breeding populations (see Table 6).

Thus, as in the case of our preferred edible plant species, we have significantly narrowed the animal food resource options available to us. Moreover, as in the case of our preferred crops, today we also rely primarily on relatively few inbred strains of certain livestock species. Only nine domesticated species provide more than 110 million metric tons of meat, with more than three-fourths of this productivity attributed to pigs and cattle alone. Poultry—chickens, turkeys, and ducks—contribute about 20 percent, with the remaining four species—sheep, goats, water buffalo, and horses—yielding less than 10 percent. Furthermore, we have not only narrowed our interspecific options for food production from animals, but we have also reduced the intraspecific genetic diversity of our preferred domesticates by allowing the extinction of the less popular or less economically productive livestock breeds. Many rare breeds of our major domesticates are extinct or currently endangered. As in the case of the attrition of our edible plant resources, such losses of animal gene resources only further impoverish our genetic heritage—a heritage that would otherwise have been richer for food production for future generations.

How important are animal foods in the human diet? First, although a great percentage of the minerals and vitamins we need can only be obtained from plants, meat can provide an easily assimilable source of energy (calories), amino acids (the building blocks of proteins), and fatty acids (the building blocks of lipids or fats), and it is relatively quick and easy to prepare for consumption. For example, whereas man directly assimilates only 53 percent of the protein in maize (corn), he assimilates 94 percent of the protein in eggs, 82 percent in milk, 70 percent in cheese, and 67 percent in beef. Moreover, in the more affluent nations, more than 50 percent of the fat in the human diet is acquired primarily from animal foods (Table 2). Although excessive meat, and therefore fat, intake may aggravate coronary disease and other health problems, fat has twice the energetic or caloric value of either starch (carbohydrates) or protein. In many of the developing nations where the per capita intake of animal foods is low, increased production of animals for food would add needed fat and protein to the human diet (Table 3). The second reason for the use of animals for food is that livestock and wild animals can be fed entirely with natural

TABLE 1. Extinct or Threatened Wild Relatives of Domesticated Mammals and Birds

Common & Latin Names	Most Recent Distribution	Conservation Status**	Domesticate(s) Related to:	Causes of Extinction or Rarity
MAMMALS				
Cattle & Relatives:				
*Aurochs *Bos primigenius*	Europe	Extinct (1627 A.D.)	*Bos* cattle *(Bos taurus & B. indicus)*	Hunted for food; competition with cattle; habitat conversion.
*Banteng (3 subspp.) *Bos javanicus/Bos (Bibos) banteng*	Borneo; Indochina; Java & Bali	Vulnerable	Bali cattle *(Bos javanicus)* & *Bos* cattle	Hunted for food; habitat loss; war; hybridization with domestic cattle.
*Gaur (3 subspp.) *Bos (Bibos) gaurus*	India, Nepal; Indochina	Vulnerable	Gayal *(B. frontalis)* & *Bos* cattle	Hunted for food and trophies; habitat conversion; cattle diseases.
Kouprey *Bos (Bibos) sauveli*	Indochina (Laos & Thailand)	Endangered	*Bos* cattle (distant relative)	Hunted for food, horns, and military sport; warfare in Indochina.
*Wild yak *Bos grunniens mutus*	Tibetan plateau; Nepal	Endangered	Domestic yak *(Bos grunniens)*	Hunted for food and hide.
*Wild Asiatic buffalo *Bubalus bubalis*	Assam, Nepal & India; Indochina	Vulnerable	Asiatic buffalo *(Bubalus bubalis)*	Hunted for food; habitat loss; competition with & diseases from cattle.
Markhor (3 subspp.) *Capra falconeri*	Pakistan, India & Afghanistan	Endangered/ Vulnerable	Domestic goat *(Capra hircus)*	Recently overhunted for food & horns; competition with domestic goats.
Pyrenean ibex *Capra pyrenaica*	Spain	Endangered	Domestic goat *(Capra hircus)*	Hunted for food & horns; hybridization with introduced subspecies.
Walia ibex *Capra walie*	Ethiopia	Endangered	Domestic goat *(Capra hircus)*	Poached for meat, horns, and trophies; recently, habitat loss.
Tibetan argali *Ovis ammon hodgsoni*	China (Tibet)	Endangered	Domestic Sheep *(Ovis aries)*	Hunted for food, sport, and profit.

TABLE 1. (Continued)

Common & Latin Names	Most Recent Distribution	Conservation Status**	Domesticate(s) Related to:	Causes of Extinction or Rarity
Mediterranean mouflon *Ovis ammon musimon*	Corsica, Cyprus & Sardinia	Endangered	Domestic sheep *(Ovis aries)*	Hunted for food & sport; predation by feral dogs; hybridization with domestic sheep.
Urial/Wild Sheep (2 subspp.) *Ovis orientalis*	Cyprus; Kashmir	Endangered	Domestic sheep *(Ovis aries)*	Hunted for food or profit; predation by dogs; diseases.
Wild Bactrian camel *Camelus bactrianus*	S.W. Mongolia & N.W. China	Vulnerable	Bactrian camel *(Camelus bactrianus)*	Hunted for food; competition with domestic livestock for water.
Vicuna *Lama vicugna*	Central Andes, South America	Vulnerable	Alpaca *(Lama pacos)*; llama & Guanaco	Hunted for fleece (wool) and meat; competition with livestock.
Pygmy hog *Sus salvanius*	Northern India	Endangered	Domestic pig *(Sus scrofa)*	Hunted for food; habitat conversion.
Horses & Relatives:				
*Wild ass (2 subspp.) *Equus asinus africanus*	Ethiopia & Somalia	Endangered (Nubian = extinct)	Ass *(Equus asinus)*; Horse *(Equus caballus)*	Hunted for meat & fat; competition with livestock; warfare; tourism.
*Tarpan/Eur. wild horse *Equus caballus ferus*	Central Europe & W. Central Asia	Extinct (1851)	Horse *(Equus caballus)*	Hunted for food.
Persian onager/Wild ass *Equus hemionus onager*	Iran & USSR	Vulnerable	Onager; also horse & ass	Habitat loss; competition with livestock; hunted for food.
Przewalski's wild horse *Equus przewalskii*	Mongolia	Probably extinct in wild	Horse *(Equus caballus)*	Loss of watering holes & habitat to domestic livestock; formerly, hunting.

TABLE 1. (Continued)

Common & Latin Names	Most Recent Distribution	Conservation Status**	Domesticate(s) Related to:	Causes of Extinction or Rarity
BIRDS				
Geese & Relatives:				
(New Zealand) Brown Teal *Anas aucklandica*	New Zealand	Vulnerable	Domestic Duck *(A. platyrhynchos domesticus)*	Habitat conversion; introduced predators; hunted for food & sport.
Madagascar Teal *Anas bernieri*	Madagascar	Vulnerable	Domestic Duck *(A. p. domesticus)*	Hunted for sport and food.
Laysan Duck *Anas laysanensis*	Hawaiian Islands (Laysan Island)	Endangered	Domestic Duck *(A. p. domesticus)*	Introduced competitors (rabbits); hunted for food & plumage.
Marianas Mallard *Anas oustaleti*	Guam & Marianas Island	Endangered	Domestic Duck *(A. p. domesticus)*	Drainage of wetland (habitat); hunted for food.
Koloa/Hawaiian Duck *Anas (p.) wyvilliana*	Hawaiian Islands (Kauai)	Vulnerable	Domestic Duck *(A. p. domesticus)*	Hunted for food & sport; introduced predators; habitat loss.
Tule White-fronted Goose *Anser albifrons elgasi*	California & Alaska, United States	Rare	Domestic Goose *(A. anser & A. cygnoides)*	Hunted for sport & food.
Nene/Hawaiian Goose *Branta sandvicensis*	Hawaiian Islands (Hawaii)	Vulnerable	Domestic Goose *(A. anser & A. cygnoides)*	Introduced predators; hunted for food.

Sources: Curry-Lindahl 1972; Gray 1954, 1971; Hyams 1972; IUCN *Red Data Book*, vol. 1 *Mammalia*, 1978, and vol. 2, *Aves*, 1978, 1979; Isaac 1970; Ziswiler 1967; also 45 FR 33768 (May 20, 1980). Although there are other threatened wild relatives of domesticated animals which could have been included, the taxa listed above were chosen on the basis of the following criteria: (1) has a domestic relative used directly or indirectly for food (or fiber) production; and (2) hybridizes successfully (and produces fertile offspring) with the domestic species or one or more of the domesticate's other close relatives.

*Indicates presumed wild progenitor of domesticated species to which it is most closely related.

**Conservation status: Classification used is same as determination in IUCN *Red Data Book*, vols. 1 & 2 (endangered = in danger of extinction; vulnerable = nearing endangered status; rare = at risk) unless the taxon was listed only on the U.S. Endangered Species list (45 FR 33768), in which case the U.S. determination was used.

TABLE 2. World Contribution of Plant and Animal Foods to the Human Diet (1974)

Food Type	Contribution of Calories: gm/capita/day	Contribution of Calories: percent	Contribution of Protein: gm/capita/day	Contribution of Protein: percent	Contribution of Fat: gm/capita/day	Contribution of Fat: percent
Plant	2121	82.6	44.6	64.6	27.1	44.0
Animal	447	17.4	24.4	35.4	34.5	56.0
Total	2568	100.0	69.0	100.0	61.6	100.0

Source: Food and Agriculture Organization of the United Nations, *1976 FAO Production Yearbook,* Vol. 30, Rome: FAO.

TABLE 3. Contribution of Plant and Animal Foods to the Human Diet: Developed vs. Developing Nations (Per Capita) (1974)

Type	Total Calories From: plants	Total Calories From: animals	Total Protein From: plants	Total Protein From: animals	Total Fat From: plants	Total Fat From: animals
Developed Nations	2216	1118	39.2	56.2	44.9	89.6
Developing Nations	2013	181	42.5	11.6	24.4	12.4
Difference	−203	−937	+3.3	−44.6	−20.5	−77.2

Source: Food and Agriculture Organization of the United Nations, *1976 FAO Production Yearbook,* Vol. 30, Rome: FAO.

TABLE 4. World Land Use Categories (1975)

Land Use Category	Hectares (1000's) (Estimated)	Total (Percentage)
Arable Cropland	1,506,139	11.5
Pastureland & Grazing	3,046,404	23.3
Forest & Woodlands	4,156,355	31.8
Other (Marginal and Desert)	4,366,428	33.4
Totals	13,075,326	100.0

Source: Food and Agriculture Organization of the United Nations, *1976 FAO Production Yearbook,* Vol. 30, Rome: FAO.

forage and browse, agricultural wastes, and certain industrial by-products that are not used by man. Over 23 percent of the dry land surface is covered by pasture or grazing lands that are basically unsuited for crop production (Table 4). There is twice as much pastureland as cropland in the world, and nearly all available cropland is already in use. Thus, domestic and wild animals, particularly ruminants such as cattle, sheep, goats, camels, and deer, will probably continue to remain our most economically and energetically efficient means of converting otherwise unusable rangeland resources into food suitable for human consumption.

Genetic Improvement of Domesticated Animals

Two major considerations of most livestock producers are: how to increase revenues by increasing the production of livestock products, and how to decrease costs by eliminating losses caused by diseases, pests, or other factors. To cope with productivity losses or cost increases, we can use an essentially technological or environmental approach characterized by antibiotics, vaccines, and pesticides, or by use of sophisticated techniques for managing livestock. The latter may include special housing or equipment that enhances productivity or facilitates survival of genetically ill-adapted animals. On the other hand, we can use a genetic approach where the aim is to improve livestock populations. In this case emphasis is placed on breeding for strains that exhibit greater productivity, better resistance to pests, or specific adaptations, e.g., to harsh or unusual climates.

In the developed nations, animal husbandry sciences have advanced considerably. Pharmaceuticals, vaccines, and other means of artificially adapting livestock to their prevailing environment have been developed. However, since simultaneous selection for both greater productivity and useful adaptations has been difficult in the past for most livestock species, the trend has been to prefer the environmental approach to the genetic one. As a consequence, the more technologically advanced nations have been very successful at developing highly productive, inbred livestock breeds for production of meat, milk, and eggs. Yet, many of these have evolved some degree of susceptibility to various pests, or they have lost their capability to genetically respond as populations to other environmental stresses. This has occurred primarily because relatively ill-adapted animals have been artificially supported, and have thus been allowed to pass on the heritable portions of their infirmities to subsequent generations. Thus, we have been unwittingly increasing the susceptibility of livestock to some diseases and pests by protecting ill-adapted individuals from the forces of natural selection. In some cases we have actually been facilitating the loss of natural adaptive capabilities within our economically preferred livestock breeds, or we have been ignoring alternative breeds that, with some genetic improvement or use in breeding programs, could be used to enhance livestock production in marginal environments.

Although vaccines, antibiotics, pesticides, air-conditioned housing, and other types of environmental alterations are usually considered more economically efficient in the short run, the consistent preference for this strategy of livestock production can ultimately produce disastrous biological consequences. Moreover, exclusive reliance on the environmental approach will become less cost-effective as more species of pathogens and pests evolve resistance to antibiotics and pesticides, while the genetic approach may become more cost-effective as costs continue to increase for veterinary services and for the oil and raw materials needed for special equipment and housing for ill-adapted livestock. Additionally, overuse of antibiotics in feed rations actually selects for antibiotic-resistant strains of livestock pathogens which may be capable of transferring their resistance traits to nonresistant pathogens of livestock or even of humans. This can cause the premature obsolescence of antibiotics important for maintenance of livestock populations as well as those important for human life and health.

These issues demand that we reexamine the viability and economic importance of the production alternatives offered by the genetic approach. As in the case of crop

improvement programs, the success of livestock genetic improvement programs will depend on the provision of genetic diversity—individuals, strains, or breeds that possess disease-resistance genes or other useful adaptations lacking in our highly productive, modern breeds. In most instances, some within-breed genetic variation exists for heritable traits of economic importance, even within our pampered and protected livestock breeds. In contrast, however, many of the less productive, "primitive" breeds are generally noted for their adaptations to particular environments and climates as well as for their resistance to livestock pests and diseases. Reliance on such genetically adapted animals in the developing nations of the tropics can be compared with their analogous use of primitive cultivars of crop species that possess disease resistance or other adaptations to the prevailing environment. In some areas of the tropics, pathogens and pests are so ubiquitous and difficult to eradicate that nonresistant livestock cannot be husbanded at all. Furthermore, in many of these countries, most of the people who raise livestock for subsistence cannot afford costly pharmaceuticals, pesticides, vaccinations, and the services of veterinarians, even when they are available. Moreover, imported, modern livestock breeds often do not exhibit the same level of productivity when introduced into tropical environments where natural forage is abundant but feed grain or feed concentrates are lacking. Or they may retain their inherited levels of productivity while suffering from the heat, cold, or lower planes of nutrition to which they are not adapted, because most livestock owners in the developing nations can scarcely afford the costly housing and cooling equipment, expensive feed rations, and constant attention and care required for most modern breeds. Under such circumstances, some productivity must often be sacrificed in order to produce food products from breeds that are typically considered "primitive" by American or European standards.

During the last few decades, livestock producers and animal breeders have shown an increasing interest in combining the best genetic traits of the modern breeds with those of some of the primitive (landrace) breeds of livestock. Crossbreeding of individuals from genetically distinct populations often results in hybrid offspring that are more "vigorous" or productive than either parent (given the same environment). In such cases of superior performance, heterosis or "hybrid vigor" has occurred as a result of the creation of novel combinations of genetic materials. Through crossbreeding, modern breeds may be able to achieve useful levels of pest resistance or hardiness, and primitive breeds—new and higher levels of productivity. For this reason, many livestock breeders are just as concerned about conservation of livestock genetic resources as many plant breeders are about the conservation of crop genetic diversity, particularly where rare and vanishing breeds are concerned.

Many breeds of all the major livestock species are rare or endangered. Of the approximately 140 European cattle breeds still in existence in 1976-1977, 107 were considered to be endangered or in a relict state within their native environment. Even more disturbing is the conservation status of most of the lesser-known primitive cattle breeds found in India, Africa, and Latin America. Although they have not been used to the same extent in genetic improvement programs as have primitive crop cultivars, many of the primitive livestock breeds have the genetic potential for enhancing the productivity of modern breeds. For example, genes for enhanced muscle growth for meat production in broilers and pigs have been provided, respectively, by a disappearing Cornish gamecock and by the Belgian landrace swine. And the highly fertile, but currently very rare, Finnish landrace sheep has been used for cross-

breeding to improve carcass conformation and yield in meat sheep breeds. Crossbreeding with prolific primitive breeds like the finnsheep can rapidly increase the efficiency of lamb meat production. In addition, primitive breeds have been and are being upgraded via infusion of genes from modern breeds. This work is particularly important for people who reside in poverty-stricken areas where it is difficult or impossible to grow crops. While some of the primitive breeds were indispensable for livestock production in centuries past, others have become better known during the last century. Some of today's fast-growing, productive beef cattle breeds like the French Charolais and the simmental, and dairy breeds like the brown Swiss were relatively unknown and little used earlier in this century. Moreover, many currently endangered or rare breeds which have fallen into disuse, such as the north Devon and Chillingham white park of Great Britain and the Texas longhorn were once relied upon almost exclusively in certain livestock-growing regions.

Heritability and Genetic Correlation

Genetic improvement is further advanced in crop plants because most are annuals and have very short generation times. However, long-lived livestock species have been considerably improved as well, particularly for yield or production characteristics and for resistance to some diseases. Genetic improvement of animal species, as with plants, depends primarily on:

- the genetic variation for the trait within available breeding stocks;
- the intensity of the selection process; and
- the heritability of the trait(s) being selected.

With regard to the first, it suffices to remark that in almost all instances where different groups within the same species have been studied, some genetic variation for the trait(s) of concern has been demonstrated. The second aspect depends on many factors, including the genetic system involved, the mating system and generation time of the species, and the financial or socioeconomic support for that particular genetic improvement program. The third consideration, refers to the ratio of the genetically induced variation to the total variation of that trait within the breeding population (the proportion of observed variation which follows family lines). Essentially then, heritability is the proportion of observed phenotypic variation that can be attributed to only genetic differences among the organisms in a population.

Only genetic variation within a breeding population can be used to permanently improve its production and adaptation characteristics. Therefore, heritability estimates, such as the examples in Table 5 indicate the potential for genetic improvement of the population(s) evaluated for that trait. Thus in chickens, the heritability of egg weight is 0.75. This means that 75 percent of the variation observed (among unrelated individuals) for egg weight in most populations has a genetic basis, whereas the remaining 25 percent of the variation is due to environmental differences. Selection for heavier eggs then should lead to significant improvement in the population(s) being selected. On the other hand, resistance to leukosis—the viral disease responsible for the greatest losses in the poultry industry for decades—has a heritability of only 0.08-0.15. Since the genetic basis of the observed variation for leukosis resistance was only about 8-15 percent, breeding for resistance to this virus should proceed more slowly.

TABLE 5. Some Heritability Estimates for Economically Useful Traits in Livestock Species*

Trait and Species/Breed	Heritability Estimate
% Solids-not-fat in milk—Ayrshire dairy cattle (1)	1.00
Front/rear index of udder proportions—dairy cattle	0.88
Egg weight—chickens (2)	0.75
Leanness of meat in pigs**	0.70
Final body weight in beef cattle (3)	0.65
Ham conformation—pigs**	0.60
Dressing percentage—American breeds of beef cattle	0.60
Body length, backfat thickness and ham weight—pigs**	0.50
Egg size—chickens	0.50
Resistance to mastitis in dairy cattle	0.38
Carcass quality points in beef cattle	0.30
Milk yield or production—dairy cattle (2)	0.30
Egg shape—chickens	0.25-0.50
Egg production—chickens (2)	0.25-0.35
Growth rate in Swedish breeds of pigs	0.26
Age at sexual maturity in chickens	0.15-0.30
Resistance to bovine leukemia in cattle (4)	0.16
Hatchability of eggs—chickens	0.10-0.15
Resistance to leukosis in chickens	0.08-0.15
Fertility in chickens	0.00-0.05
Left/right index of udder proportions—dairy cattle	0.00

*All data taken from Johansson and Rendel (1968) unless noted otherwise.
**Data calculated for pigs slaughtered after reaching 90 kg liveweight.
Additional References: (1) Wilcox, et al. 1971; (2) Lerner and Libby 1976; (3) Lindhé 1974 and (4) Ernst, et al. 1974 in Sindicato Nacional de Ganadería de España.

A low heritability does not imply that selection for that trait will necessarily be a worthless endeavor. For instance, in the case of poultry leukosis, selection among strains of white leghorn for over 20 years led to the development of a highly resistant, low mortality line as well as a very susceptible, high mortality line. At the beginning of this experiment, mortality due to leukosis in the unselected leghorns was about 14 percent. After 15-20 years of selection, mortality in the resistant strain was down to 1-4 percent; yet, in the highly susceptible line, mortality had risen from 14 percent to 56 percent. Moreover, since the resistant strains were also being selected for greater egg production and lower mortality rates due to all causes, the leukosis-resistant lines were capable of producing nearly as many eggs as the most highly productive but nonresistant strain. The income per chick was $2.46 for the latter line and $2.40 per chick for the resistant lines. In comparison, the mean income from 25 randomly chosen nonresistant lines was only $2.03.

Another consideration in animal genetic improvement programs is the genetic correlation between economically desirable traits being simultaneously selected. Two traits are genetically correlated if selection for one trait automatically brings about a nonenvironmentally (i.e., genetically) related change in the other. In a study of five dairy cattle breeds in the United States, for example, genetic correlation between milk yield and protein yield was found to be very high and positive for all breeds. Thus, selection for increased production of milk automatically led to increased pro-

duction of protein. This would have been expected; however, the negative genetic correlation between milk yield and the actual percentage of protein in the milk was not. This correlation was low to moderate, ranging from -0.11 for brown Swiss cattle to -0.55 for Jersey cattle. Therefore, even though selection for increased milk yield increases protein yield, the actual percent protein in the total volume of the milk tends to decline as productivity increases. This may serve to explain why the Holstein breed, which has been the most intensively selected for yield characteristics (and consequently has become the breed most widely used for milk production in the United States), has the lowest percent protein in its milk. Thus, exclusive selection for only a single trait, e.g., yield or productivity, can often lead to the loss of other economically desirable characteristics within the livestock population being selected.

Estimates of heritabilities should be interpreted with extreme caution. They usually vary from population to population within the same species, resulting partly from differences in the genetic make-up of the populations and partly from differences in their respective environments or management regimes.

Breeding for Resistance and Hardiness

This section discusses uses of intraspecific genetic diversity, that is, genetic differences among individuals, strains, or breeds of a particular livestock species. The only exception to this generalization used here is that of domesticated *Bos* cattle. Most modern European and American breeds are known as *Bos taurus.* And although some people consider all *Bos* cattle as members of this species, most researchers do not. Thus, the humped zebu cattle breeds of India are usually known as *Bos indicus,* and breeds such as the brown cow of Switzerland and the rare north Devon are sometimes referred to as *Bos longifrons* or *brachyceros.* However, offspring of crosses between any individuals of these cattle species are viable and fully fertile. Most zoologists today consider all *Bos* cattle "species" or breeds to have descended from a single wild progenitor—the now extinct aurochs (*Bos primigenius*). For these reasons, all species of *Bos* cattle are herein considered together.

Disease and Insect Resistance

Many of the rare, primitive or landrace breeds of livestock are noted for their resistance to diseases and insect pests. The N'Dama cattle of Nigeria in West Africa are well known for their high degree of tolerance to sleeping sickness (trypanosomiasis), as are the West African shorthorns of the Gold Coast (Ghana). The N'Dama breed is rare and the West African shorthorn is in danger of extinction primarily because it is no longer preferred for meat production in its homeland. Yet both breeds may be of value for enhancing the adaptability of cattle in areas infested by the tsetse fly, the vector for the trypanosomes which cause sleeping sickness. The Chillingham herd of the rare white park cattle of Great Britain are reputed to be free of brucellosis and mastitis, and the animals show little evidence of internal parasites. The once endangered Texas longhorn has also been acknowledged for its resistance to certain diseases and pests that plague the southwestern U.S. cattle-growing regions. And Fayoumi chickens are resistant to leukosis; they have already been used to produce a new breed of egg-laying chickens called "Dokki IV." The new breed,

created by crossing the Fayoumi with the barred rock, has become widely distributed throughout the Near East.

Although the unique disease and pest resistance qualities of such rare and primitive breeds of livestock are often cited as reasons for their conservation, three counterarguments have been raised:

- In contrast to the situation for most crop species, the occurrence of single resistance genes is rare in most animal species;
- With few exceptions, e.g., trypanosomiasis resistance, veterinary or pharmaceutical control of pests is quicker and more effective for treatment of most of the larger livestock species;
- In poultry, disease resistance may not necessarily be more common in primitive than in modern breeds.

Doubtless these arguments have some validity, but consider the following. As for the first counterargument, even though it is definitely easier for the animal breeder to locate and hence use single gene resistance, exclusive or extensive reliance on this option in crop breeding has actually encouraged the development of gene-for-gene relationships between crops and their native pests or diseases. Since single gene resistance factors tend to be easily overcome by coevolved crop pests (with but a few known exceptions), many plant breeders believe that reliance on single gene resistance only enhances the vulnerability of our crops to major pest outbreaks or disease epidemics. Many of these same problems are likely to apply to animal breeding as well. Furthermore, disease resistance characteristics typically have low to moderate heritabilities, usually due to polygenic inheritance or the additive (cumulative) effects of many genes. And resistance to infectious diseases in animal species is more likely to be controlled by polygenic inheritance than by one gene. Yet, selection for traits controlled by many genes can often be an economically worthwhile endeavor.

Mastitis, the most economically disastrous disease of the dairy cattle industry today, is caused by a number of different species of bacteria that infect the udder and teats of individual animals. Resistance to it is most probably controlled by the additive effects of many genes. However, within a single generation, selection for resistant cows and their progeny, and against susceptible cows, resulted in a 33-38 percent reduction in its incidence within an experimental population. Similarly, resistance to one of the worst diseases afflicting honeybees, American foulbrood (*Bacillus larvae*), has also been attributed to the effects of many genes. Two different recessive genes appear to control the behavior of adult worker bees in resistant strains; one controls their behavior for uncapping wax cells which contain infected larvae (young), the other their behavior for removing infected larvae from the hive. Strains are resistant only if they are homozygous for both genes simultaneously, i.e., if they inherit only one trait or the other, they will only be able to uncap the wax cells or to remove larvae but not both. Furthermore, resistance of the larvae *per se* to infection by spores of the bacterium is a trait that may itself be controlled polygenically (by the additive effects of many genes).

A third example is avian leukosis, a virally induced cancer. Leukosis in chickens is caused by one or several subgroup viruses, and resistance to each subgroup is believed to be controlled by a pair of genes. Although heritability of leukosis resistance tends to be rather low, selection for resistance in two strains of white leghorns reduced leukosis mortality from 14 percent in 1935 to 0.9 percent in one

strain and 3.7 percent in another by 1967—94 percent and 74 percent reductions, respectively. In contrast, a strain selected for susceptibility increased from 14 percent to 55.7 percent mortality—about a 300 percent increase. Moreover, the best resistance levels in the resistant strains were attained earlier in the experiment and could probably have been achieved more quickly had the stocks been better managed and the breeders been selecting only for leukosis resistance. They were, however, simultaneously breeding for a number of polygenic traits, including increased egg production, greater egg weight, and lower mortality from all causes. An 80 percent reduction in overall mortality, from an average of 48 percent in 1936 to 10 percent in 1967, was achieved. At the termination of this experiment, the leukosis-resistant strains returned a greater profit per chick started than the average of 25 random entries of nonresistant but very productive white leghorn strains. More recent experiments have shown that a high degree of resistance to one of the leukosis subgroup viruses can be achieved by intensive selection for only two or three generations. In one experiment mortality was reduced by more than 85 percent in one strain and 25 percent in another within only three generations.

These three examples demonstrate that selection for polygenically inherited resistance can be successful and economically profitable, even when heritability of the trait is low. Other examples than those cited could have been provided, e.g., atrophic rhinitis in swine and bovine leukemia in cattle. Even though it is easier to transfer single-gene resistance among breeds, the beneficial effects of polygenically inherited traits can also be transferred via crossbreeding, backcrossing, and further selection.

The second counterargument states that veterinary and pharmaceutical control is generally preferable to genetic control for larger livestock species. In the short run, pesticides and vaccines are usually more cost-effective than selection for natural resistance in livestock, or development of other biological control options. But unlike the latter methods, the former ones suppress the discovery of truly resistant individuals while they protect the genetically ill-adapted or infirm animals. Moreover, antibiotics and pesticides affect "good" as well as "bad" pathogens and pests. Widespread use of pesticides will not only cause the evolution of pesticide-resistant pests, but will also severely affect survival of the natural predators and diseases that might otherwise have been available to assist in controlling them. Likewise, once a pest organism has evolved resistance to a particular antibiotic, further use of the prescribed drug will only suppress any drug-sensitive, beneficial predators or bacterial competitors of the harmful pathogen.

Another more important danger is the potential threat to human life and health from the overuse of antibiotics in livestock feed. Bacteria may obtain resistance to antibiotics and other drugs in a variety of ways. One recently discovered yet little understood mechanism is the tranfer of plasmids which contain resistance factors, usually called R factors. A plasmid is a circular piece of genetic material which is independent of the principal chromosome within a bacterium. R factors can exhibit a remarkably wide range of bacterial and even viral hosts. They may cross species-specific barriers, i.e., resistance may be transferred between different species (or genera) of microorganisms, or they may even be environmentally acquired by bacteria through exposure to a medium containing plasmids. For example, an R factor for streptomycin resistance may originate in a *Shigella* species of bacteria, such as the one responsible for human bacillary dysentery, as a result of the extensive use of that antibiotic for treatment of the disease. Then the resistance could be transferred

(e.g., by a bacterial virus) to an *Escherichia coli* bacterium, such as the *E. coli* in the human gut. From there the R factor for streptomycin resistance might be transferred again, this time to a species of *Salmonella* bacteria present in the human gut. Usually R factors carry multiple resistance to many different antibiotics. A type of R factor originally found in a bacillary dysentery bacterium determines multiple resistance to sulfonamides, streptomycin, chloramphenicol, and tetracyclines—all of which have been used to treat this disease. Soon after the discovery of this resistant enterobacterial species, many other multiply resistant enterobacteria appeared. That they had obtained resistance to all of these antibiotics simultaneously suggests that an R factor or plasmid from a resistant carrier species was responsible.

Transference of R factors from one species of bacterium to another, perhaps completely unrelated species has brought about untoward consequences when using the same antibiotics to treat both animals and people. We already have evidence that drug resistance obtained in a strain of cattle *Salmonella typhimurium* (type 29) was probably transferred to a human *S. typhimurium* species. An enteritis epidemic occurred among cattle in Great Britain during 1964-1966. The outbreak was attributed to the evolution of resistance to the antibiotics that were being routinely given to the affected livestock via their feed. Immediately following this outbreak, the resistance was evidently transferred to the human bacterium. Hundreds of people were infected and five died. As a result of this epidemic, a British joint committee (known as the Swann Committee) recommended that antibiotics used specifically to treat human disease be prohibited from use in livestock feed; these recommendations were adopted in England in 1971.

As for the third and final counterargument, it should be noted that even though the disease resistance traits of primitive breeds of poultry are perhaps no more prevalent than in the more productive, modern breeds, rare and primitive poultry breeds may still possess useful heritable traits that may one day be of value to the poultry industry. Moreover, in many instances, the animal genetic resources that are still available for conservation and use have not been appropriately evaluated. We should allow rare breeds to disappear only when adequate evidence has been presented that they are inferior in most circumstances. Nevertheless, most primitive breeds have yet to be adequately evaluated. In the past, the choice of a breed for economic purposes has been based on superficial knowledge rather than on an objective comparative evaluation. And oftentimes, evaluations have been one-sided, dealing only with one or two economic traits which have not been measured appropriately. Until rare and endangered primitive livestock breeds have been more carefully evaluated for performance and economic value, it would be imprudent to ignore the potential importance of any of them.

Particular breeds or populations of livestock may possess heritable traits which may not be directly related to disease or pest resistance *per se*, yet which may indirectly contribute to the resistant qualities of the individual animal. As an example, disease resistance in the zebu (*Bos indicus*) breeds of cattle is partly related to their short-haired, shiny coat which makes it more difficult for ticks and other parasites (or their eggs or young) to attach to the animal. In addition, their hide is thicker and less susceptible to such parasites. When introduced European and zebu (Afrikander) cattle were mixed together in tropical pastures, the European cattle had 2-7 times the number of disease-carrying ticks per unit of body surface area as the Afrikander. Moreover during a 30-month period, mortality due to tick-transmitted heart-water

disease (*Cowdria ruminantium*) averaged 60.7 percent for the European cattle, whereas it averaged only 5.3 percent for the Afrikander cattle. Breeds such as the Texas longhorn and many zebu cattle have been observed to exhibit certain behaviors that reduce infestations of screwworm fly. Whereas most modern breeds of cattle tend to remain at or near watering areas where adult screwworm flies often concentrate, the longhorn and zebu cattle drink and leave watering holes, or they obtain much of their water from browse. Oftentimes, characteristics such as these are extremely important in determining the overall resistance of an animal to pests; yet they may be easily overlooked during the initial phases of an evaluation or genetic improvement process.

Harsh Environments

With respect to the livestock industry, the term harsh environments refers to an array of unfavorable conditions that are typically coincident with arid or wet, hot subtropical and tropical regions, or with extreme cold, salinity, or other severe physical factors. Globally, the adaptability of livestock to tropical environments is of great importance for overall availability of livestock products. Nearly 50 percent of the cattle in the world reside in the tropics, as do 15-20 percent of all swine. Moreover, most of the world's sheep and goat population is concentrated in semi-arid areas north and south of the tropical latitudes.

In spite of the great numbers of livestock in tropical and semi-arid or arid environments, their productivity in these regions is very low. In the developing nations in particular, 60 percent of the world's livestock population produces only 20 percent of the total animal production for the 70 percent of the world's human population who live in these countries. In part this low productivity must be attributed to the harshness of the environment *per se*, including the lack of forage in arid lands and the increased incidence of diseases and pests in tropical latitudes. However, much of it is due to a lack of intensive management practices and the use of well adapted indigenous breeds that are genetically inferior in terms of productivity when compared with more modern breeds. For example, some studies have demonstrated that modern European breeds of cattle (*Bos taurus*) are capable of outperforming more heat-adapted zebu breeds (*Bos indicus*) when reared in tropical or subtropical environments. However, the ill-adapted European livestock had to be supported by expensive, labor-intensive management practices, and they showed definite signs of heat-stress, including a much higher respiration rate and laborious breathing. In addition, feed grain is scarce in tropical regions since almost all of it must be used to feed people rather than livestock. The European livestock perform well only with high levels of nutrition, i.e., a diet that typically contains expensive feeds, grains, and concentrates. When both types of cattle are fed on an equal but lower plane of nutrition, the indigenous livestock usually show higher productivity, greater fecundity, and better survival rates than the exotic European breeds. For instance, in Zambia the zebu breeds outperformed Hereford cattle when both were fed on pasture, while the reverse was true on the feedlot. Livestock management in the tropics is usually minimal since people have neither the time nor money to invest in exotic breeds that must be protected from harsh conditions. Thus, breeds that have lower water requirements and better heat-tolerance, and that can more efficiently utilize available browse and forage will continue to be preferred in most of these countries.

Many of the rare, landrace livestock breeds are noted for their unusual or unique adaptations to harsh environments, just as they are often noted for their disease- or pest-resistance qualities. The North Ronaldsay sheep of the Scottish coast and the cladore sheep of the western coast of Ireland principally eat seaweed. These rare and unique breeds have become physiologically adapted to coastal environments and this unusual type of forage. Like many marine organisms, their blood and milk contain high levels of iodine and urea. The endangered Kuri cattle which inhabit the islands and shores of Lake Chad in Africa can also eat course vegetation. But unlike any other known livestock breed, many have spongy, buoy-shaped horns which provide buoyancy while swimming to new grazing areas. This breed, an exceptionally good milk producer, is one of the few remaining nonhumped (i.e., non-zebu) cattle breeds left in North Africa. In the past, all of the cattle from this region were of this type; but today all of the original nonhumped breeds are extinct except the Kuri, the N'Dama, and a few others. Perhaps breeds such as the Kuri could be more extensively used to enhance livestock productivity, particularly for inland lake, coastal, and island environments.

In spite of the potentialities of these unique breeds, most livestock owners in the world do not use such grazing or forage areas. A majority, however, do pasture animals on sparsely vegetated areas which often contain many browse or shrub species and few grasses and forbs. Only a small proportion of the livestock producers in the world can afford to buy feed grains which require the expense of fuel oils for their production. As oil, and hence feed grain, prices continue to rise, producers even in the developed nations will begin to reconsider the economic potential of some of the better-adapted, lesser-known livestock breeds and their crossbred progeny. These animals are capable of producing meat and milk from natural browse and forage alone. As an example, the rare short-tailed sheep of northern Europe live on sparse vegetation and shrubs, and their offspring show a predilection for browse over grasses even when they contain only 1/8 short-tailed blood.

The Texas longhorn (Fig. 4) is perhaps the best example of a breed adapted to utilize natural browse and forage. Longhorns were the first cattle introduced to America. As a result of centuries of natural selection in hot, semi-arid climates, this breed adapted well to the plant resources and harsh environments of the southwestern United States. Until the latter part of the 19th century, the hardy, adaptable, and aggressive Texas longhorn served as the basis of the southern and western U.S. cattle industries. As no other beef cattle breed has done since, the longhorn dominated the North American beef industry. Near the turn of the century more fashionable British beef breeds, such as the Hereford and shorthorn, were introduced to the United States; protected by barbed wire and other new management practices, these breeds quickly replaced the hardy longhorns. By 1900 the typical, purebred longhorn had almost disappeared as a result of "genetic swamping" through crossbreeding (primarily unintentional) with the "improved" exotic breeds. Thus, the longhorns imparted a portion of their pest resistance qualities, hardiness, and browse capabilities to the more productive English beef breeds.

Just as the breed was nearing extinction, a few interested persons pushed for its preservation in the late 1920's. The U.S. government set aside wildlife refuges in Nebraska and Oklahoma for the few remaining feral animals, and some southwestern cattlemen began to maintain small herds. The introduced British breeds were so ill-adapted to the physical environment and climate in some of the cattle-growing

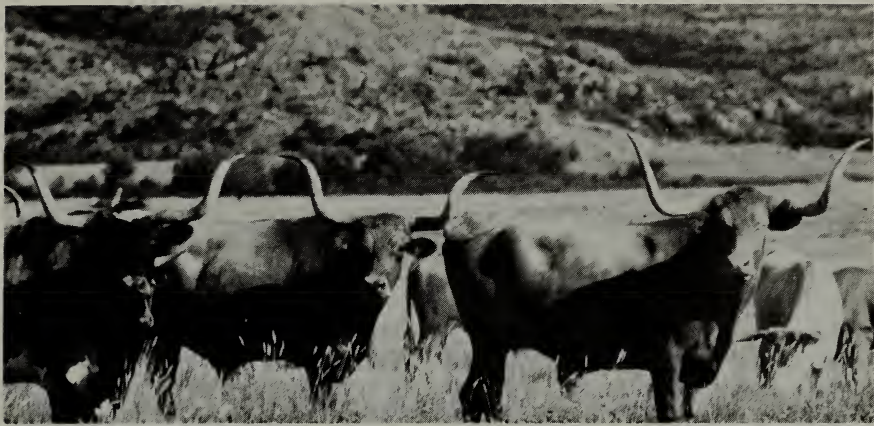


Fig. 4. A modern herd of longhorn cattle in Texas. (Photo: U.S. Fish and Wildlife Service, USDI)

regions that a better-adapted zebu cattle breed, the Brahman, had to be imported to upgrade their adaptability. The Brahman supplied the necessary hardiness the British breeds lacked, and that the longhorn breed would probably have supplied if it had been more appropriately used for crossbreeding before it neared extinction. Crossbreeding the Brahman with the exotic cattle produced the Santa Gertrudis and other part-zeboid cattle that have become familiar to many cattlemen in the United States. In a similar vein, the Texas longhorn, rescued from the brink of extinction, may be used in the near future to produce new breeds that are better adapted to the southwestern U.S. climates. Old rare breeds such as the Texas longhorn probably possess genes or linked gene combinations that may provide essential characteristics desired in the future. For example, longhorns are very fertile, calve easily, and typically exhibit heterosis when crossbred with Herefords and other modern breeds.

The rare breeds have not been utilized to any great extent for crossbreeding primarily because most are relatively unknown, and partly because they are so rare. However, we can examine some of the benefits that may accrue from crossbreeding highly productive American or European cattle breeds with common but less known zebu (*Bos indicus*) breeds. From the results of such crossbreeding experiments, we might be able to ascertain the potential value of some of the rarer breeds for enhancing livestock productivity, particularly in marginal environments. The zebu cattle of India are morphologically and physiologically better adapted to heat than are most *Bos taurus* breeds. Their light-colored, shiny coat effectively reflects sunlight; and the short hairs facilitate dissipation of heat. Coat color is highly heritable and genetically correlated with heat-adaptedness in many livestock populations. Zebu cattle also have a large dewlap and hump which allows them a greater surface area per liveweight than the modern cattle breeds. Typically their respiration rates increase less rapidly as the ambient temperature rises.

When crossbred with modern breeds, zebu cattle usually produce heat-tolerant offspring that have better carcass and yield qualities than their zebu parents. An excellent example is the Canchim breed developed in Brazil over the last few decades. It was derived from a cross between the very productive Charolais breed of France and an Indo-Brazilian strain of zebu cattle in the ratio of 5/8 Charolais to 3/8 zebu

blood. The Canchim animals are much more resistant to heat (and ectoparasites) than their Charolais ancestors, and they make better use of the natural rangeland resources available to them. Their hair is short, shiny, and light-colored, while the skin around the mucous membranes is generally dark, so that they better tolerate full sunlight than Charolais stock. Whereas the fertility of purebred Charolais suffers in tropical environments, the Canchim hybrids perform very well. In fact, the breed shows some evidence of heterosis for fertility traits; the 1/2 and 3/4 Charolais-zebu animals have fertility rates of 69 percent and 63 percent respectively, while the Charolais animals demonstrate a rate of about 30 percent and the Indo-Brazilian zebu, 43 percent. On the other hand, the Canchim crossbred progeny have inherited the yield, carcass quality, and fast-growth characteristics of their Charolais ancestors. The average daily weight gain of Canchim males was 558 g (1.23 lb), as compared with 615 g (1.35 lb) for purebred Charolais and only 372 g (0.82 lb) for the Indo-Brazilian zebu. Canchim females averaged 467 g (1.03 lb) per day in comparison to 509 g (1.12 lb) for Charolais and only 367 g (0.81 lb) for zebu females.

A variety of zebu breeds have also been crossbred in India and Africa to produce dairy cattle that are more productive yet better adapted to either dry or humid tropical climates than are the modern dairy breeds from which they were derived. However, in a study conducted in Kenya, crossbred offspring of a zeboid breed and the highly productive, indigenous Sahiwal were preferred over progeny of crosses between zebu and modern breed cattle. The modern breeding stock was judged incapable of realizing its full genetic potential in Kenya's heat.

Discussion about the potential for genetic improvement of modern breeds via crossbreeding with landrace breeds need not be limited to zebu cattle. The tropical dairy criollo cattle of Latin America are also well-adapted to tropical environments. The criollo have very short hair and fewer hair follicles per skin area than do either zebu or European cattle breeds; their skin is very thick and possesses numerous sweat glands. Their conformation and wide, well-formed and pigmented hooves allow them to walk fast under scorching sunlight—one of their most noted and valuable qualities. The criollo is known for its high fertility despite the harsh tropical environments in which it lives. Yet even when crossed with U.S. Holstein cattle, the F_1 criollo hybrids nearly matched purebred Holsteins in dairy milk yield and outperformed either of the purebred parents in fertility.

Additionally, a number of rare or uncommon primitive breeds of sheep have been noted for meat production as well as for their adaptation to tropical environments. The indigenous sheep of Sri Lanka—the woolless jaffna—are hardy, resistant to pests and diseases, prolific, and well adapted to the hot, humid climate of that country. Likewise, the priangan and East Javan fat-tailed breeds from Indonesia are noted for their high reproductive rates and heat-adaptedness. In both Sri Lanka and Indonesia imported breeds had lower fertility and higher mortality than indigenous breeds, primarily because they were not adapted to the prevailing diseases, pests, and climate. Many other highly prolific, woolless meat breeds of sheep have been selected for productivity and adaptability in arid environments. These include the mandya, Sudan Desert, and blackhead Persian. An early-maturing, arid-adapted, woolless meat breed, the dorper, was developed by crossing Somali or South African blackhead Persian sheep with a more productive, modern breed, the Dorset horn. The dorper is particularly well-adapted to dry regions which have spiny vegetation.

A number of other rare breeds that possess special adaptations have been suggested for study, evaluation, or preservation.

Rare or unique breeds of livestock may be utilized directly or indirectly (for crossbreeding) to enhance meat production in arid or other harsh environments. But wild species of animals may be used as well. In fact, the production potential of wild animal herds composed of many different species can exceed the meat production obtained from conventional livestock breeds, often with less detrimental impact on rangeland resources.

Food Production and Wild Animal Species

Wild animal species can be used directly as sources of food or indirectly as breeding stock for the genetic improvement of closely related, domesticated species. Close relatives probably played an important role in the evolution of our domesticates, both as the original donors of their genetic constitution, i.e., as wild progenitors, and as sources of other heritable characteristics derived from occasional outcrossings between domesticated and wild animals. Some traditional agricultural peoples still encourage and exploit such crosses. For example, the Tsembaga in New Guinea rear domesticated sows and only castrated males; they release their sows into the forest to be inseminated by feral boars. The Naga of Assam place salt-licks in the forest to attract wild gaur bulls to inseminate their gayal cows. And in Sri Lanka and Assam, matings between wild bulls and domesticated cows of the Asiatic buffalo (*Bubalus bubalis*) are tolerated. These practices can be likened to those of many traditional agriculturalists in regions of crop genetic diversity, where wild and weedy relatives of crop plants are allowed to remain in or near cultivated fields. In this way, new genes or gene complexes that may confer pest resistance, hardiness, or other useful qualities can be introduced into domesticated stocks and the best adapted or most desirable hybrid offspring can be retained as future breeding stock.

When directly used for food, wild animal species often provide an ecologically and economically more efficient means of producing meat and other edible products from marginal environments than do husbanded domestic livestock. This point is especially pertinent for desert, tundra, or marine environments as well as marginal tropical environments. For example, in the seas and oceans where we do not husband domesticated livestock, the primary productivity or "grass" consists of a variety of minute plant and animal species called plankton. This productivity cannot be directly harvested economically to produce desirable human foodstuffs. It is therefore most efficiently utilized by harvesting marine animals, which feed on the plankton or plankton-feeders.

Yet even in terrestrial environments where domesticates can be reared and more easily cared for, the productivity derived from mixed crops of wild animals is often greater. For example, East African savannas will support a biomass of wild ungulates at some 6-8 tons/km^2 (15-20 tons/mi^2). However, the same grazing area will support barely 2.3 tons/km^2 (5.9 tons/mi^2) of cattle biomass, with the highest figures of well managed ranches at 4.6 tons/km^2 (11.8 tons/mi^2). The reasons why a higher standing crop of wild species can be maintained over that of domesticated livestock in such environments are manifold. Wild African ungulates appear to com-

monly out-perform domesticates in many ways; they are generally:

- More resistant to pests and diseases;
- Better adapted to heat and drought;
- Complementary in their diet and feeding habits;
- Able to gain weight faster on unimproved pastures, especially in arid and semi-arid environments;
- Better meat producers (yield slightly higher percent carcass); and
- Superior in their reproductive potential.

The tsetse fly species of tropical Africa that carries African sleeping sickness is illustrative. Its range covers an area the size of the United States, yet the native wild animal populations of antelope, buffalo and other bushmeat species are totally resistant to sleeping sickness. In contrast, none of the highly productive, modern livestock breeds and very few of the primitive breeds are even tolerant of trypanosomiasis. Although it is possible to obtain tolerant cattle hybrids by crossing susceptible, modern breeds with tolerant primitive breeds, it seems more reasonable to retain habitats infested with tsetse fly for the management and controlled harvesting of game species. At the very least, tolerant livestock should be pastured along with wild animals, rather than being used to entirely replace them. It is significant to note that areas infested by the tsetse fly constitute most of the remaining sizeable game reserves in Africa. In addition to these considerations, wild animals are typically better at converting available forage to biomass while producing leaner meat. Thus, mixed herds of wild game animals do not destroy fragile environments as do livestock species, and most marginal environments are ecologically fragile. In arid and semi-arid regions such as the great Kalahari Desert in southwestern Africa, large herds of gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), eland (*Taurotragus oryx*), and other antelope species have been protected in the Kalahari Gemsbok National Park since 1931. These great game animal herds thrive in the desert and on adjoining semi-arid lands. They have lived there on very meager pastures for a very long time, while more recently introduced domesticates have severely overgrazed adjacent arid savannas, open grasslands, and sand dune areas.

When populations of wild animals are properly managed and conserved or are husbanded in a semi-domesticated state on game ranches, they can provide much more meat or food per unit area in marginal agricultural environments than conventional livestock. However, when they are not effectively managed or if they are harvested wastefully and indiscriminately, they are vulnerable to depletion or extinction. Table 6 provides a mere sample of the multitude of currently endangered or extinct species that have attained their nonrenewable resource status primarily because of their food value for humans. When so many potentially renewable genetic resources are driven to extinction or reduced to such low numbers, much of the potential for long-term economic productivity derived from the earth's land and water resources is forever lost. It is a mistake to assume that other potentially useful biota will automatically take the place of extinct species.

Throughout history, humans have established economical enterprises based on the extraction of one or a group of wild species. In a few instances, populations managed on a sustained yield basis have enabled the long-term existence of human settlements and economic activities in environments otherwise inhospitable to man. These successful endeavors have not only produced food products for local or global trade, but have also allowed the conservation of habitats and other species not

TABLE 6. Some Threatened or Extinct Animals Used Principally for Food

Common & Latin Names	Conservation Status Recent Distribution	Causes of Extinction or Rarity
FISH:		
Amur sturgeon *Acipenser shrencki*	Endangered USSR	Commercial overfishing.
Lake sturgeon *Acipenser fulvescens*	Endangered Great Lakes, U.S.	Overfishing; also often killed for damaging fishing gear.
Kaluga *Huso dauricus*	Endangered Amur River, USSR	Commercial overfishing for caviar and flesh.
Ala balik *Salmo platycephalus*	Endangered Turkey	Overfishing.
REPTILES:		
River terrapin/Tuntong *Batagur baska*	Endangered S.E. Asia—rivers	Hunted for meat, oil & eggs; habitat loss.
Galapagos tortoise *Testudo elephantopus* (12 subspecies)	Endangered Galapagos Islands	Killed for meat & oil by whalers, sealers, buccaneers & fishermen; introd. competitors & predators.
Green sea turtle *Chelonia mydas*	Endangered Tropical oceans	Hunted for meat, eggs & oil; skin sometimes used also.
Terecay turtle *Podocnemis unifilis*	Vulnerable No. South America	Hunted for meat & eggs; commercially exploited for market.
Ground iguana *Cyclura* spp. (5 spp./8 subspp.)	Endangered to Rare West Indies	Hunted for food, also for zoo trade & sport; habitat loss; introduced predators.
BIRDS:		
Ducks & Geese:		
Madagascar Teal *Anas bernieri*	Vulnerable Madagascar	Hunted for food and sport.
Tule White-fronted Goose *Anser albifrons elgasi*	Rare United States	Hunted for food and sport.
Brush Turkeys:		
Gray's Brush Turkey/Maleo *Macrocephalon maleo*	Vulnerable Indonesia	Overcollection of eggs, formerly hunted for meat.
Shorebirds:		
Eskimo Curlew *Numenius borealis*	Endangered Alaska & E. U.S. shores	Hunted for food, pleasure & sport; habitat destruction.
Auks:		
Great Auk *Pinguinus impennis*	Extinct (1844) N. Atlantic coast	Hunted for meat & eggs; young used for fishing bait.

TABLE 6. (Continued)

Common & Latin Names	Conservation Status Recent Distribution	Causes of Extinction or Rarity
Pigeons & Relatives:		
Passenger Pigeon *Ectopistes migratorius*	Extinct (1914) E. North America	Hunted for food, sport & pleasure; habitat loss.
Dodo *Raphus cucullatus*	Extinct (1681) Mauritius	Hunted for food; introduced predators (pigs).
Parrots & Relatives:		
Imperial Amazon *Amazona imperialis*	Endangered Dominica, W. Indies	Hunted for food; destruction of tropical forests.
MAMMALS:		
Primates:		
Yellow-tailed woolly monkey *Lagothrix flavicauda*	Endangered Peru	Hunted for food & skins; habitat destruction.
Douc langur *Pygathrix nemaeus*	Endangered Southeast Asia	Hunted for meat; recently, habitat loss—Indochina war.
Whales:		
Blue whale *Balaenoptera musculus*	Endangered Oceans	Hunted for edible oil & meat; also baleen & bone.
Fin whale *Balaenoptera physalus*	Vulnerable Oceans	Hunted for edible oil & meat; also baleen & bone.
Humpback whale *Megaptera novaeangliae*	Endangered Oceans & coasts	Hunted for edible oil & meat.
Sea Cows & Manatees:		
Dugong *Dugong dugon*	Vulnerable Indo-Pacific coasts	Hunted for meat & oil; also for hides and tusks.
Steller's sea cow *Hydrodamalis stelleri*	Extinct (1768) Bering Islands	Hunted for meat & oil.
Manatee (3 species) *Trichechus* spp.	Endangered/ Vulnerable Africa, America	Hunted for meat & oil; also for bones & hides.
Horses & Relatives:		
Quagga *Equus quagga*	Extinct (1878) South Africa	Hunted for meat & hide; combatted as livestock competitor.
Cattle & Relatives:		
Pigmy hippopotamus *Choeropsis liberiensis*	Vulnerable West Africa	Hunted for bushmeat; habitat destruction (logging).

TABLE 6. (Continued)

Common & Latin Names	Conservation Status Recent Distribution	Causes of Extinction or Rarity
North Andean huemul *Hippocamelus antisensis*	Vulnerable Andes, S. America	Hunted for meat; loss of habitat (agriculture & grazing).
Western giant eland *Taurotragus d. derbianus*	Endangered West Africa	Hunted for meat; introduced animal diseases (rinderpest).
Wild yak *Bos grunniens*	Endangered Nepal & Tibetan plateau	Hunted for meat & hide.
Lechwe (3 subspp.) *Kobus leche*	Vulnerable Southern Africa	Market & subsistence hunting; some habitat loss.
Arabian oryx *Oryx leucoryx*	Endangered—Oman, Arabian peninsula	Hunted for meat, leather, & medicinal purposes.
Addax *Addax nasomaculatus*	Vulnerable Sahara desert	Hunted for meat, hide, & sport.
Dorcas gazelle (3 subspp.) *Gazella dorcas*	Endangered N.W. Africa; Arabia	Hunted for meat & sport; overgrazing by livestock.
Mediterranean mouflon *Ovis ammon musimon*	Endangered Cyprus, Corsica, Sardinia	Hunted for meat; feral dog predation; habitat destruction.

Sources: Curry-Lindahl, 1972; IUCN *Red Data Book,* vols. 1-4.

directly valued for economic purposes. However, the opposite trend has all too often prevailed, that is, the ultimate result is extinction of the food species followed by commercial extinction of the economic endeavor involved. Some species have been overexploited to provide sources of food to support other economic activities. For example, the Galapagos Island fauna, especially many of the huge Galapagos tortoises and the land and marine iguanas, were esteemed by sailors, merchantmen, whalers, sealers, and buccaneers in the 18th and 19th centuries. The islands were frequently employed as stopping points or permanent sites for economic enterprises until the native food species became so depleted that the islands could no longer support these activities. Goats and other competing domestic animals introduced as meat producing substitutes overgrazed the islands, and they only further exacerbated the depletion of the well-adapted, native fauna.

In most instances, endangered species that provide edible products, e.g., most of those listed in Table 6, have been overharvested as a direct consequence of the food production process (Fig. 5). An excellent example is the extinct Passenger Pigeon (*Ectopistes migratorius*) (Fig. 6) of North America. This game bird was not only relished by sport hunters over most of the eastern United States since early colonial times, but it also provided the basis of a commercial squab industry in the northeastern states. The latter enterprise was made possible by the establishment, around 1850, of railroads which facilitated the rapid transport of hundreds of thousands to

Fig. 5. Before the 1849 Gold Rush, the tule elk *(Cervus elaphus nannodes)* was very abundant. Nearly exterminated by hunters, it was reduced to a single relict population at Buttonwillow, CA. This subspecies is now restricted primarily to semi-arid habitats in scattered populations throughout California. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI)

millions of birds from remote nesting areas to city markets and restaurants. During the latter half of the 19th century, the pigeon trade became highly organized. The livelihood of at least seven large, commercial dealers (commission houses) depended on the extraction and sale of wild pigeons. Unfortunately, the ease of transport and thoroughly organized trade brought about the downfall of both the species and the industry based upon it. Whereas an estimated 3 billion Passenger Pigeons existed on the North American continent at the time of the arrival of the first European colonists (possibly 25-40 percent of the total U.S. bird population at that time), by 1915 not a single individual remained. No other terrestrial American game species has ever formed the basis of such a lucrative commercial enterprise. Although wild turkey, bear, squirrels, and a few other game species probably now consume the acorns, beechnuts, and other wild foods the Passenger Pigeon once consumed, none of these species has even approached the commercial importance of the extinguished species.

It is especially tragic that many seabirds, fish, sea turtles, and marine mammals, e.g., whales and sea cows, historically sought for food or sources of commercial sea products are now endangered or extinct (Fig. 7). These losses cannot be replaced by domesticates, nor have other commercially valuable taxa taken their place. Consider the large species of baleen whales, harvested primarily for their edible oil which is used to make margarine and cooking oils, and secondarily for their meat. The three principal economic species, the blue, humpback, and fin whales, have suffered heavily from overharvesting and today all three are threatened. As illustrated in (Fig. 8) total world production of baleen whale oil declined dramatically between

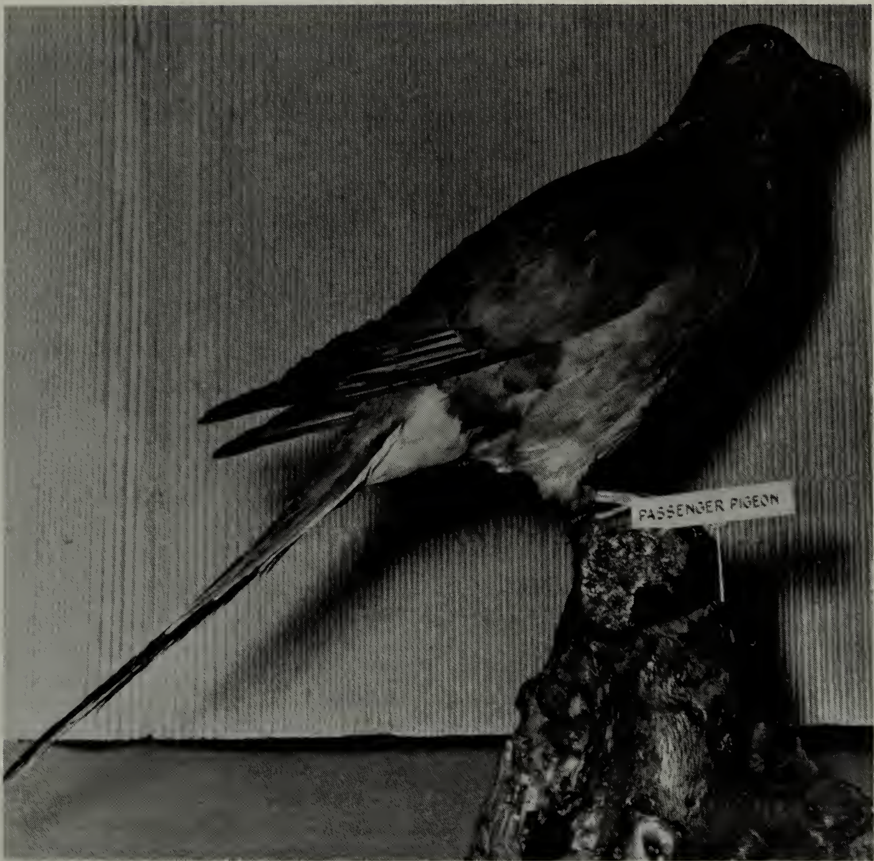


Fig. 6. A specimen of the extinct Passenger Pigeon *(Ectopistes migratorius),* a species that once supported a thriving commercial squab industry in the United States. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI)

1948 and 1976. And as Fig. 9 illustrates, as the most valuable and largest species (in fact, the largest animal on earth today)—the blue whale (*Balaenoptera musculus*), and the humpback whale (*Megaptera novaeangliae*) both declined due to overharvesting, the next most commercially valuable species—the fin whale (*B. physalus*)—principally supported the whaling industry. Finally, with the decline of the fin whale, the least commercially valuable species—the sei whale— supported the baleen whale industry until it neared commercial extinction. Although no whale species has yet been totally exterminated as a result of commercial whaling, many past economic enterprises based on genetically distinct populations have reached or neared commercial extinction as a result of the exhaustion of available whale stocks.

For the most part, commercial overharvesting of wild species for food occurs as a result of economic activities conducted by modern, industrialized societies. However, in the developing nations, hunger and poaching of animals to provide food as well as luxury items for international export has contributed heavily to the indis-

Fig. 7. The green sea turtle *(Chelonia mydas)* is distributed throughout tropical seas; it is currently endangered primarily as a result of the food value of its eggs and flesh. (Photo: C. Harrison, U.S. Fish and Wildlife Service, USDI)

criminate slaughter of wild animals. For example, in West Africa most of the large game animals have already been exterminated. In Ghana the pigmy hippopotamus *(Choeropsis liberinsis)* and the West African manatee *(Trichechus senegalensis)* have been driven to extinction, and the green colobus monkey (*Colobus verus*) and ebiana palm-squirrel (*Ebixerus ebii*) are now endangered. In the Ivory Coast, monkeys have practically disappeared, save a few populations in faunal reserves. Because monkey flesh is usually preferred over other meats, the great demand has led to high prices for meat from primates. For example, at a local market in Zaire in 1976, a small monkey carcass cost $7. As prices for bushmeat have risen, so too has the tally of population extinctions. Rare, endangered, or threatened species are often harvested in the developing nations for meat, and in many cases, for meat and other products such as furs, skins, ivory, and folk medicinal products that fetch very high prices in legal or illegal markets. Examples of such abuse include black jaguar *(Panthera onca)* and giant anteater *(Myrmecophaga tridactyla)* in Brazil, the African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) in southern Africa, and the black lechwe (*Kobus leche smithemani*) of Lake Bangweulu in Zambia. Heavy poaching of animals in West Africa and other less developed nations is often associated with high demands for bushmeat and the lucrative trade in luxury items derived from wildlife—products typically sold to tourists or consumers from the more affluent nations. Additionally, poachers and trappers often snare individuals of nontarget species; for example, trapping for bushmeat in Africa has been a factor in the decline of the mountain gorilla (*Gorilla g. beringei*) and other endangered species.

In addition to the direct extermination of food resource populations, agricultural activities, such as the extension of agricultural lands (Fig. 10) and overgrazing, are also taking a heavy toll on wildlife. Ill-adapted cattle and other livestock species have virtually replaced stable communities of up to 50 or more wild animal species wherever ranching and agricultural expansion has occurred. Along with the influx of

Fig. 8. World production of baleen whale oil, 1947-1976* (Source: International Whaling Statistics) *Computed by subtracting world production of sperm oil from world production of all whale oil, and multiplying the number of barrels by 170kg/barrel.

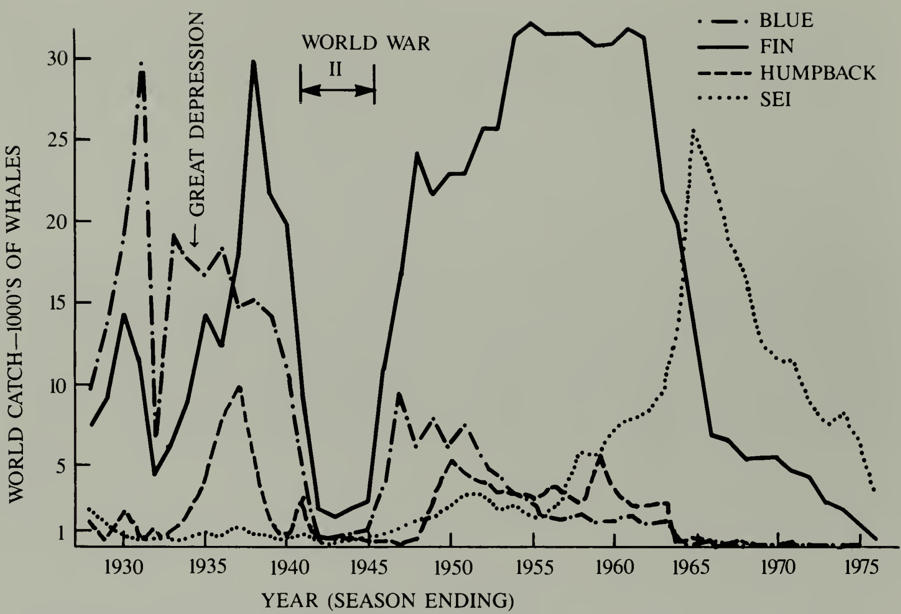


Fig. 9. Total world catch of blue, fin, humpback, and sei whales, 1928-1976. (Source: International Whaling Statistics)

Fig. 10. The Whooping Crane *(Grus americana)* was once hunted for food and sport, but is now endangered and formally protected. Although it has been valued as a source of food, loss or alteration of its habitat—primarily for agricultural expansion—has been the greatest threat to its survival. Today only a single flock of this large white and black crane, which has a wing span of more than 7 feet a maturity, still exists. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI)

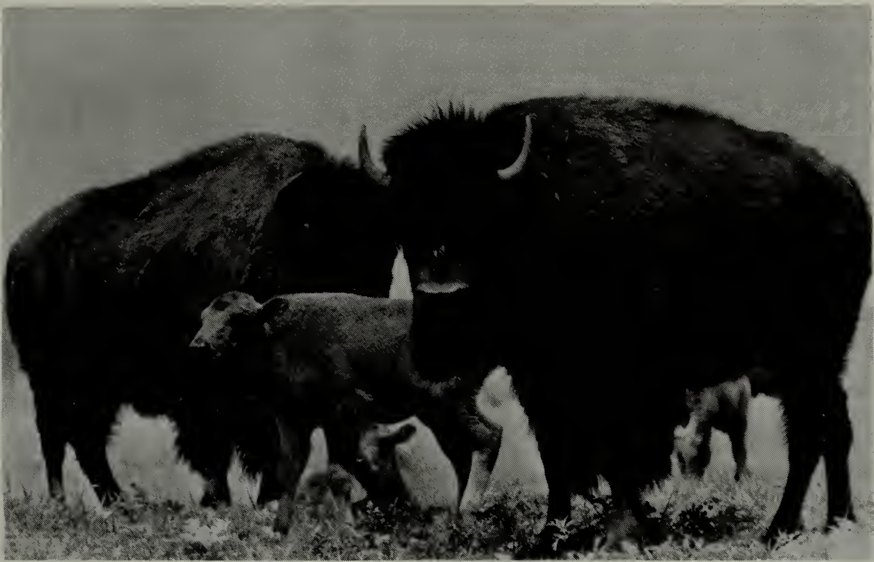


Fig. 11. As in the case of the Texas longhorn cattle, the American buffalo was saved from near extinction by the interest and efforts of a few people. As a result of their concern, the gene pool resources of this species have persisted, and recently have been employed in the development of the American breed—a hardy, pest-resistant cattle × bison hybrid. (Photo: E.P. Haddon, U.S. Fish and Wildlife Service, USDI)

livestock, exotic animal diseases have been introduced. These have often precipitated the decline or extinction of wildlife populations, e.g., Asiatic wild ass subspecies and the giant eland. Cattle plague (rinderpest) swept the African continent, and exterminated native antelope and water buffalo populations in many areas. In addition, because productivity of livestock is so low, wild species are often viewed as competitors (or predators) of livestock, and many have been eliminated partly for this reason as well, e.g., the quagga and some zebra species. Much of this displacement of valuable, well-adapted wild meat-producing species has been founded on a cultural rather than an economic or ecological basis. In fact, as noted previously, often a mixed crop of wild animal species is the more reasonable option—at least for most marginal agricultural environments. In the final analysis, the most economically efficient use of available land and water resources for food production will occur only when experimentation and evaluation of the best mixture of both wild and domesticated species is conducted in specific areas.

Wild Species and the Genetic Improvement of Domesticates

Wild animals have been employed far less frequently than wild or weedy plants for the genetic improvement of our preferred domesticates. A major reason for this is that the offspring from crosses between different, but closely related animal species are often sterile or less fertile, particularly if the number of chromosomes in the genome differs for each. Typical examples of sterility problems with interspecific

animal hybrids include the mule and hinny (horse x jackass)—males and females which are both virtually sterile; and the yakow and chowri (yak x cattle)—males are functionally sterile but females are fertile. In spite of low fertility or sterility problems, the hybrids from these interspecific crosses are often considered superior to either of their parents for particular uses.

A relatively new interspecific cross is that between the threatened (once endangered) American buffalo (*Bison bison*) (Fig. 11) and domesticated cattle. The reputed hybrid offspring of such a cross have been variously termed ''cattalo,'' ''beefalo,'' and ''the American breed.'' Apparently, however, only the cattalo and American breed animals have been substantiated as authentic descendants of a bison x cattle cross. The authenticity of the so-called beefalo has not yet been upheld by blood-typing evidence.

As in the case of the yak x cattle crosses, half-bison males are usually completely sterile while the hybrid females are fully fertile. At present, the only fertile, true-breeding animals which legitimately contain bison blood are those of the American breed. They are 1/2 Brahman, 1/4 Charolais, 1/8 bison, and 1/16 each of Hereford and shorthorn. These cattle grow fast, calve easily and thrive on alkaline, coarse sacaton grasslands in the arid southwestern United States. They reputedly produce leaner meat, and have natural resistance to flies, ticks, lice, and other parasites, as well as freedom from diseases such as pinkeye and cancer. They are reputed to be able to walk farther to water, and to survive better in hilly, rocky terrain than most other cattle. This breed combines some of the best meat-producing characteristics of some of our modern breeds with the disease resistance and hardiness of zebu cattle and bison.

The potential usefulness of the new American breed of cattle suggests that interspecific crosses between closely related species might be useful for other species as well. In particular, genetic improvement of the Domestic Goose (*Anser anser*) and Chinese Swan Goose (*Anser cygnoides*), and the Domestic Duck (*Anas platyrhynchos domesticus*), by hybridization with related wild species is a distinct and relatively unrecognized possibility. About 33 species and subspecies of wild geese belong to the genera *Anser* and *Branta,* and many of these will produce fertile hybrid offspring when crossed with the domesticated geese. Similarly, most of the 50 or more species of *Anas* will produce fecund progeny when crossed with the Domestic Duck, a descendent of the Mallard (*Anas platyrhynchos*).

In particular, three threatened species might one day be useful for genetically improving these domesticated, nonmigratory birds, all of which were derived from wild, temperate-zone species (see Table 1). As such, the domesticates possess substantial amounts of subcutaneous fat deposits below the swimline for insulating purposes, thus reducing the percentage of meat that can be obtained from the carcass. In contrast, the threatened species, the Nene or Hawaiian Goose (*Branta sandvicensis*) (Fig. 12), the Laysan Duck (*Anas laysanensis*) (Fig. 13), and the Koloa or Hawaiian Duck (*Anas (platyrhynchos) wyvilliana*) are all tropical species. Thus, they have probably not evolved layers of insulating fat as have temperate species. In addition, they all have long laying seasons, and most tropical species of these genera are reputed to continue laying when moved to temperate latitudes. The adaptable Koloa, in particular, is reported to breed from December to May; however, it may actually breed year-round, since eggs and ducklings have been found in all months except August. Moreover, the Nene inhabits waterless, upland environments, and the

Laysan Duck can survive without fresh water and only rarely swims; since both are well adapted to terrestrial rather than aquatic life, they copulate effectively on land. If the latter trait could be passed on to the domesticated species, it would obviate the need for sizeable water areas for successful breeding. In contrast to the preferred avian domesticates (chickens and turkeys), ducks and geese also typically require far less animal protein in their diet and thus are capable of living primarily on vegetation. Yet they are often considered less desirable as meat-producing species, partly because of their above-mentioned disadvantages. Through greater utilization of such related wild species, the undesirable traits of these domesticates might be reduced or eliminated.

Wild Species as a Source of Food

In the United States and most developed nations, wild animals are hunted primarily for sport and pleasure, and only secondarily for meat. However, in many of the developing countries of the world, wild species are an essential source of food for most people. Additionally, harvesting or game ranching of wild animals provides export commodities that are important for national gross productivity, as well as a

Fig. 12. The threatened Nene (Hawaiian) Goose *(Branta sandvicensis)* is distantly related to the Gray Lag-Goose *(Anser anser)* and the Chinese Goose *(Anser cygnoides),* the presumed wild ancestors of two different species of domesticated geese. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI)

Fig. 13. A pair of endangered Laysan Ducks *(Anas laysanensis).* Believed to be the rarest duck in the world, the Laysan Duck exists in the wild only on Laysan Island. (Photo: D.M. Marshall, U.S. Fish and Wildlife Service, USDI)

source of income for a great number of people who would otherwise be unemployed.

In Peru, trade in anchovy and other fish products accounts for a very large portion of its total export trade. In 1965, a very poor harvesting year due to unfavorable weather conditions, commercial exports of fish products were valued at $180 million, which accounted for 25 percent of Peru's total exports. In addition, murres, puffins, and other seabirds are often harvested commercially as well as consumed locally. The muttonbird industry of Australia is based on Slender-billed Shearwaters (*Puffinus tenuirostris*) which bring local harvesters some $70,000 annually for their meat alone.

Export trade in game meat is, at present, less significant worldwide than trade in fisheries commodities. In 1978, 55,000 metric tons of game meat valued at $140 million were traded internationally, with the supply expected to increase substantially in 1979. However, in many regions of Latin America and Africa game is an essential source of protein and calories in the human diet, just as marine species supply a significant part of the diet of many island or coastal peoples. In such countries as Botswana, Zaire, and in the northern Ivory Coast, game is the primary source of animal protein. About 73 percent of the local meat consumed in Ghana is derived from wild animals. And roughly 75 percent of the people who live south of the advancing Sahara Desert rely on wildlife for food, including game, snails, caterpillars

and other insects. In Botswana, more than 50 species of wild animals are harvested for food; all in all, a great variety of animal species are taken for food throughout the developing nations.

Furthermore, harvesting of game has become an increasingly important source of national revenues over the last decade. For example, total revenues from exploitation of wildlife in Botswana rose from about $600,000 in 1966 to around $10 million in 1973. In 1972 more than $8.6 million was derived from both traditional and sport harvesting of game. About half of these revenues pertained to the use and value of the animals as a source of food for local markets. The other half related specifically to the direct and indirect expenditures of hunters, photographers, and other tourists, e.g., for ivory and other products, trophies, and safari company revenues. Over a one and one-half-year period, a single market in Accra, Ghana sold a total of $160,000 worth of local game meat at an average price of $1/kg ($0.45/lb). In West Africa in general, bushmeat usually fetches a much higher price in urban markets than meat from domesticates. Similarly, meat from wild animals also commands a higher price in the Federal Republic of Germany and other European countries due to its allegedly better flavor. In the late 1970's retail prices of the best cuts of imported red deer venison (*Cervus elaphus*) were priced as high as beef fillet at $11/kg ($5/lb), while domestic, fresh venison has recently been priced at $6.50 - $8.00/kg ($2.95-$3.65/lb), twice the price of beef or lamb.

Much of this domestic and imported game is derived from game ranching concerns where wild species are reared in a semidomesticated fashion, i.e., where the breeding, feeding, and harvesting of the animals is controlled by man. Deer farming or ranching is currently being conducted in West Germany, Sweden, and Australia; and prices for breeding stock have been steadily climbing. For example, in West Germany the cost of one breeding fallow deer has risen from about $270 in 1976 to between $650 and $800 in early 1979; although their weight is a tenth that of cattle, current prices for these semidomesticated animals are half that of comparable cattle breeding stock. The trend also prevails in Australia; in late 1978, the price of one breeding red deer was as high as $1130, and of rusa deer, $565.

Game ranching in the developing nations is also becoming more popular. Some African species which have shown potential for semidomestication or game ranching include a rodent, the grass cutter (*Thryonomys swinderianus*), and various species of ungulates, such as the springbok (*Antidorcas marsupialis*), the eland (*Taurotragus oryx*), and the African buffalo (*Syncerus caffer*). In the Transvaal of South Africa, about 3,000 herds of springbok and blesbok (once endangered) with a minimum combined population of over 300,000 animals, are being raised along with cattle. By 1964, more than 4,000 ranches in this area were involved in commercial exploitation of such game species. Other wild species, such as the oryx of Africa and the capybara of Latin America, are also being used on game ranching concerns. The oryx (gemsbok) (*Oryx gazella*) has great potential for use in semi-arid regions of the tropics. It requires only half the water a drought-adapted dorper sheep does, and a quarter of that required by indigenous boran cattle (adjusted for metabolic weight). Thus, during droughts, the oryx can gain weight on forage that is insufficient for weight gain in indigenous African cattle. In addition, the oryx, with a 57 percent cold-dressed carcass weight, yields a greater quantity of meat per liveweight than cattle (52 percent). Moreover, in 1975 oryx meat sold for $1.14/kg ($0.52/lb), whereas beef sold for $0.86/kg ($0.39/lb). And hides, trophy heads, or horns from the oryx

return additional income for game producers. All things considered, the value of oryx as a game species was calculated at $233 per ranch animal unit, while cattle returned $157 and dorper sheep, only $77. Considering the value and usefulness of this African oryx species, it is most unfortunate that the splendid Arabian oryx (*O. leucoryx*) is now an endangered species. This game animal once ranged across the entire Arabian peninsula and was perhaps the most valuable source of food in the deserts of the Middle East. Less than 200 of these drought-adapted game animals now exist, their decline being the result of overhunting by motorized hunting parties and local Bedouin tribesmen armed with modern firearms. In addition, the beautiful scimitar-horned oryx (*O. dammah*)—a species adapted to semi-arid environments surrounding the Sahara desert—is also nearing endangered status due to its value for food and competition from domestic livestock.

A species which has considerable potential for meat production in the humid tropics is the capybara *(Hydrochoerus hydrochaeris),* a relative of the domesticated guinea pig. About the size of a small domesticated pig, the capybara has long been exploited as a food species in Latin America. It was originally domesticated by the Piaroas Indians. Well adapted to very humid environments with high ambient temperatures, it is currently being used as a semidomesticated species on game ranches in Venezuela's flooded savannas. It feeds primarily on grasses and aquatic weeds, including water hyacinth (*Eichhornia* spp.); and of all the nonruminating herbivores, it is superior in its capabilities to digest forage, even tough and fibrous vegetation. Its reproductive performance is superior to that of other domesticates in humid tropical regions, e.g., in the flood plain savannas it is 6 times as efficient in producing food as cattle. Thus the yearly harvesting rate for capybara can reach 40 percent without affecting the long-term yield potential of the herd; in comparison, cattle can withstand only 9-11 percent yearly extraction rates in comparable habitats. Whereas cattle production yields only 14 kg of meat annually from each hectare (12.3 lb/acre) of flooded Venezuelan grasslands, game ranching of capybara returns 64 kg/ha/year (56 lb/acre/year). On one ranch that raised both cattle and capybara, the net cash return from capybara was 3 times that derived from cattle—an average of $11/ha ($4.45/acre) for capybara as compared with $4/ha ($1.62/acre) for cattle. As evidenced by the recent evaluations of the underutilized but substantial productivity of the oryx and capybara, the unrecognized potential of these and other wild meat-producing animals remains to be adequately investigated. Experimentation with the domestication and use of wild species on game ranches should be encouraged in the tropics where there is an abundance of economically useful animal genetic resources. Such experimental game ranches might be supported and encouraged by local or national governments or groups of livestock producers interested in enhancing the productivity of their available rangeland resources.

4

Medicinal Plant and Animal Resources

Today, about half the world's medicinal compounds are still derived or obtained from plants. Medicinal products from biota are generally more important in the developing nations of the world than they are in the United States and other industrialized nations. However, even in the developed nations which tend to focus on chemical discovery and synthesis of pharmaceuticals, biotic drug products are major contributors to the human health services sector of the economy. In addition to their restorative effects, pharmaceuticals that contain plant- and animal-derived medicinals currently contribute billions of dollars to the U.S. economy each year. More than 41 percent of all 1973 over-the-counter prescriptions in the United States contained an active ingredient derived from wild or cultivated flora and fauna. Fully 25 percent of all these prescriptions contained essential active ingredients derived from angiosperms (higher plants), and sold for an estimated retail value of $1.6 billion; preliminary data for 1980 indicated an estimated value of more than $4 billion. Additionally, microbial products contributed 13 percent and animal products, about 3 percent. If one considers the drugs dispensed from government agencies, hospitals, and other legitimate channels, the retail value of all legally dispensed, community prescriptions containing at least one higher plant product was about $3 billion in 1973 ($8.1 billion on the basis of preliminary data for 1980). It would be difficult to estimate the contribution of natural sources to the nonprescription drug market (including veterinary and illegal drugs)—though the figure would be staggering. Moreover, the indirect contributions of plants and animals to the drug development process, e.g., uses of biota as research tools or models and for drug safety testing, defy economic calculation, despite the fact that without them most modern drugs would not be available nor could they be used with any assurance of safety.

The demand for biotic drug products has remained stable over the last two decades even though investments for research and development of new, naturally derived pharmaceuticals decreased substantially during that time. One important reason for

the sustained demand for many natural drug compounds is that cultivation or harvesting of medicinal biota is often less costly than artifical drug synthesis. For example, less than 10 percent of the 76 drug compounds present in higher plants that were used in 1973 U.S. prescriptions were produced commercially by total chemical synthesis. Even though nearly all of these natural compounds have been successfully synthesized artificially, their direct extraction from natural sources is usually less costly. As an example, consider the alkaloid reserpine—the first tranquilizer used in the United States; reserpine is obtained from serpent-wood (*Rauvolfia* spp.)—evergreen shrubs found in tropical forests. Rauwolfia root extracts have been used in India for at least 4,000 years to treat mental illness and nervous disorders. However, the active root alkaloids were not recognized as potentially valuable plant drugs by Western scientists until the 1940's, and drug products derived from them were not actually marketed in the United States until a decade later. Yet within a few years, reserpine had become almost universally adopted as a tranquilizer and treatment for schizophrenia, mild hypertension, and anxiety. By 1967, almost 82 percent of the antihypertension drugs prescribed in the United States (2.67 percent of all community drug prescriptions) contained reserpine or other serpent-wood extracts. In recent years, the annual retail value of reserpine alone has exceeded $30 million. However, the cost would have exceeded an estimated $50 million each year in the absence of tropical sources of serpent-wood extracts. The primary reason is the difficulty of artificially synthesizing reserpine. In the mid-1970's, a multistep, synthetic process yielded the drug at $1.25/g, while commercial extraction from natural sources produced the drug for only $0.75/g. Other drugs that cannot be produced economically by industrial synthesis include codeine, morphine, digoxin, and atropine.

Additionally, it is often cheaper to use natural extracts as building blocks for the synthesis of "semisynthetic" drugs. For example, plant saponins can be extracted and easily altered chemically to produce sapogenins for the manufacture of steroidal drugs. The world steroidal drug market is currently worth about $1 billion annually at the consumer level, and steroids were present in one out of seven community prescriptions dispensed in the United States in 1973. In recent years, 95 percent of all steroids have been obtained from extracts of tropical, saponin-containing yams (*Dioscorea* spp.) which yield diosgenin and other useful sapogenins after minor chemical alterations. Diosgenin is commonly used in the manufacture of sex hormones (e.g., androgens, estrogens, progesterone), oral contraceptives, and cortisone and other anti-inflammatory drugs. During the mid-1970's, an estimated 1,350 tons of diosgenin was being used worldwide each year. Mexico has historically been the largest producer; in 1974, tropical Mexico produced about 600 tons of diosgenin at a cost of $27.70/kg ($12.60/lb), or about $15 million worth. Two years later the same quantity of Mexican diosgenin was valued at almost $83 million ($152.20/kg or $69.10/lb). Even though wild sources of yams are becoming depleted and cultivation is an expensive procedure, natural sources of diosgenin and other steroid precursors will remain important until a more cost-effective means of synthesizing steroids has been developed. Since the latter possibility is not likely on a large scale in the foreseeable future, depletion of wild dioscorea stands has encouraged a renewed emphasis on locating other plant steroid precursors and microorganisms capable of facilitating their conversion.

A second major reason for the sustained demand for natural drug products is that they often serve as chemical "blueprints" for the development of related syn-

thetic drugs. Since the chemical structures and stereochemistry of natural, pharmacologically active compounds are usually very complex, their *a priori* chemical synthesis is unlikely without the use of such natural model compounds. For example, cocaine, from the tropical shrub *Erythroxylum coca,* provided the chemical structure used for the synthesis of procaine and other related local anesthetics. Similarly, semisynthetic penicillin derivatives which can counteract the immunity enzymes produced by penicillin-resistant bacterial strains were obtained by studying the natural molecule. Other examples include morphine and codeine, alkaloids from opium poppies (*Papaver somniferum* and *P. bracteatum*), which have been used to develop synthetic pain-killers, and the tropane alkaloids (e.g. atropine, scopolamine) which were utilized for the development of a large number of synthetic anticholinergic drugs. Many drug researchers believe that the provision of these blueprints or chemical models for the development of synthetics is the most important function of newly discovered medicinal plant compounds. However, such artificially derived drugs have seldom exceeded the effectiveness of their parent compounds.

Extensive study of these issues reveals that natural extraction and artificial synthesis of modern drug compounds are actually complementary research efforts. Yet at present, they are typically not perceived as such, and natural drug research still receives relatively little attention or support from most major pharmaceutical firms in the United States. Ironically, one important reason for this has been the success of technological innovations in the industrialized nations which have allowed the artificial synthesis of chemicals that mimic the effects of their natural counterparts. Such innovations have led to a preponderance of synthetic drugs in pharmaceutical markets during the last half century. Artificially synthesized drugs do have certain advantages over drug compounds extracted from natural sources. For example, medicinally useful biota are often difficult to domesticate or cultivate. They may require specific habitats, e.g., shaded, humid tropical environments, or they are often sparsely located in the wild, particularly if natural populations have suffered from overharvesting. Moreover, direct application or use of natural medicinals may produce undesirable side effects. Since most natural drugs are derived from poisonous plants or animals and since they frequently vary in potency and toxicity, synthesis usually allows greater control over purity and dosage effects. Thus, artificial synthesis of similar drug compounds can actually overcome many of the toxic effects experienced with the use of natural drugs, and this is one reason, in addition to economic considerations, why it has been such a boon to the pharmaceutical industry. Once a successful natural compound has been located and studied, an amazing array of chemical substitutes or molecularly altered natural compounds can often be easily and cheaply produced in the laboratory. During the first half of this century, the displacement of natural drugs by their synthetics reduced our dependency on imported vegetal or animal products, many of which came from distant tropical areas. Unfortunately, however, it simultaneously produced a trend towards the deemphasis on exploration for and location of new biotic sources of medicinal agents.

Yet, in spite of the displacement and attrition of drug compounds derived from natural sources during the last century, particularly in the United States and other industrialized nations, today interest in plant- and animal-derived drugs is being revived. One reason for this renewed interest is the necessity of replacing drugs that have lost their effectiveness for combating the specific diseases for which they were developed. Over time pathogenic organisms usually evolve immunity or new virulence

mechanisms which counteract the effects of the pharmaceutical compounds employed against them. Other reasons for the renewed interest in natural products include: the discovery of penicillin and other valuable microbial antibiotics; the success of the rauwolfia drugs of India for treatment of various mental disorders and hypertension, a success story which focused more attention on the value of folkloric medicine and ethnobotanical studies; the discovery of hallucinogenic plant drugs for the study of mental disorders; and, the recent emphasis on interdisciplinary and international research efforts. Along with this resurgence of interest, a "natural" drug revolution has occurred during the last few decades. A multitude of works by ethnobotanists, anthropologists, and zoologists has appeared in recent years. Additionally, a number of symposia and meetings on the exploration for and potential use of novel plant- and animal-derived drug substances has resulted in some surprising discoveries of new medicinal compounds. Furthermore, novel approaches, such as searching through herbarium specimens to locate drug plants unknown to industrialized societies, should facilitate our search for new biotic drug sources.

In spite of the plethora of recent research efforts and a number of promising new natural drugs and drug compounds, inertia within the drug industry has generally inhibited the use of this accumulated knowledge for the development of natural pharmaceutical compounds. Much of the apathy toward natural drug research has been attributed to relatively recent unsuccessful industry-sponsored efforts. Various difficulties—most of which could have been easily remedied—caused these initial attempts to fail, and the modest investments of money, time, and effort were not repaid by useful results. Future success with such efforts will require different attitudes and approaches than those that have been commonly assumed by drug firms and their researchers. Moreover, as illustrated by the more than 400 patents issued in 1975 for drug substances isolated from angiosperms alone, the continuance of such attitudes will thwart progress in natural drug research.

The impending destruction of a wealth of potential drug compounds available from natural sources demands that this inertia be overcome, for with each passing year many unknown or uninvestigated species become extinct or endangered. Medicinally useful chemicals found within biota are ultimately produced as a result of gene action. Thus, alkaloids, glycosides, and other pharmacologically active natural compounds cannot be considered apart from the genes and the organisms responsible for their production. In addition, the tremendous value of nonhuman primates as animal models for drug testing and research is based primarily on similarities between the genetic constitutions of these species and humans. The significance of such medicinally useful biota as gene resources is that they are vulnerable to extinction due to overharvesting or excessive habitat loss. And a significant proportion of the world's medicinal genetic heritage exists in the tropics where habitat alterations and destruction of natural environments has accelerated tremendously during the last few decades. Habitat conversion is also responsible for the loss of much of the world's human cultural diversity, and indigenous knowledge of medicinal compounds from plants and animals is still one of our most important means for discovery of unknown biotic drug sources. Just as the true value of biotically rich natural environments and the medicinal gene resources they harbor is finally being perceived, they are being irretrievably lost at an ever-increasing rate. *In situ* conservation of such natural genetic reservoirs is our only key to arrest this tide of destruction, for it is the best means of conserving the wild species which harbor

potentially useful drug compounds and the evolutionary processes which create and maintain these chemicals. Failure to attend to the threats of tropical deforestation and the accelerating rates of species extinctions will result in significant economic productivity losses in the pharmaceutical and health services industries, both now and in the future.

Medicinal Gene Resources Currently In Use

A multitude of species of plants, fungi, animals, and microbes produce pharmacologically active substances currently used in Western medicine. In fact, natural drug compounds are so common and well known that standard pharmacology textbooks list plant-derived drug prototypes to illustrate the classical effects of drugs for most of the major pharmaceutical categories. Yet, most forms of life remain to be investigated systematically for their medicinal value, and natural drug research remains a very low priority. Even the potentialities of mankind's major source of medicinal and all other economically useful biota—the angiosperms or flowering ("higher") plants—have been examined only superficially. In spite of this, at least eight new drugs from higher plants—including reserpine, vincristine, and vinblastine—have been introduced to the U.S. prescription drug market since 1954.

Products from Plants and Fungi

Table 1 provides a list of the most important plants and fungi currently used medicinally; all of the plants listed are vascular plants (Division Tracheophyta), and the fungi are sac fungi (Division Ascomycota). It is interesting to note that ancient or folkloric uses of these major medicinal species usually predated their more modern or recent applications. Consider ergot or smut-of-rye (*Claviceps purpurea*) (Fig. 1), a member of a family of sac fungi, a parasite that infests the grain of rye and a few other grasses. For many centuries prior to its adoption by the Western world in the 17th century, Chinese and European midwives used ergot concoctions to speed delivery and to slow or stop hemorrhaging during and after childbirth. Ergot was not used in obstetrical practice *per se* until the late 18th century. Although it is no longer an approved drug in the United States, it has been replaced by some of its alkaloids, especially ergonovine—a drug valued even more than the animal hormone oxytocin. Ergonovine is particularly valuable in cases of hemorrhage, and is sometimes employed after cesarean operations. Similarly, even though the discovery and use of *Penicillium* molds as sources of antibiotics is basically a 20th century phenomenon, the Chinese recognized the medicinal value of green (blue) molds for curing festering ulcers as long ago as 2000 B.C., and ancient Egyptians often applied moldy bread to open wounds. Probably the most familiar of our modern antibiotics is penicillin—the first to be isolated. It was initially obtained in 1929 from the species *Penicillium notatum*, which was found contaminating a *Staphylococcus aureus* bacterial culture. However, penicillin yields from this species were very low, and consequently, the drug was expensive when human drug trials were initiated in 1941. When World War II began, there was a great need to reduce production costs and make penicillin more readily available for Allied troops. Fortunately, a USDA researcher discovered *Penicillium chrysogenum* (Fig. 2) growing on a moldy cantaloupe in a market in

TABLE 1. Folk and Modern Uses of Some Major Medicinal Fungi and Plants

FUNGI (Division Ascomycota):

Species and Common Name	Active Ingredients	Family
Claviceps purpurea ergot smut-of-rye	ergot alkaloids including: ergonovine ergotamine	Ergot (Sac fungi) (Clavicipitaceae)

Ergot was employed for centuries by Chinese midwives to stop hemorrhaging. In the 17th century it was adopted by the western world, and in the 18th century was first used in obstetrics; by the early 19th century it was official in most pharmacopoeias. We now use ergonovine in the final stages of labor or after childbirth, especially for hemorrhaging; it is sometimes administered after caesarean sections. It is also used for migraine headaches, as is ergotamine. Dilhydroergotoxine is a vasodilator used to counter hypertension and peripheral vascular diseases, and is also somewhat effective in treating senility.

Penicillium chrysogenum *Penicillium notatum*	penicillin and other derivatives	Aspergillus (Aspergillaceae)
Penicillium griseofulvum *Penicillium patulum*	griseofulvin	
Penicillin molds		

The use of green (blue) molds for their antibiotic properties probably originated in the Orient more than 3,000 years ago. Chinese, Egyptian, and Indian physicians commonly employed molds (and yeasts) on open wounds, inflammations, boils and other infections, and on skin afflictions such as eczema, as long ago as 1000-2000 B.C. Molds were also employed by the Greeks and Romans up until the Renaissance, after which they were seldom mentioned until the late 19th century. However, the bactericidal properties of mold fungi were not formally known in modern medicine until 1929 when Sir Alexander Fleming and his associates reported the inhibition of *Stapholococcus* bacteria by *Penicillium notatum.* During World War II, the more productive species, *P. chrysogenum,* was discovered; today most of the penicillin antibiotics used worldwide are obtained from genetically improved strains of this species. Penicillin and other natural or synthetic penicillin derivatives are used to effect cures in cases of anthrax, pneumonias, meningitis, diptheria, tetanus, syphilis, and gonorrheal, streptococcal, and other bacterial infections. Griseofulvin, an anti-fungal compound originally extracted from *P. griseofulvum,* is used for tinea fungus diseases of the skin, such as ringworm and athlete's foot. Today this compound is obtained from improved strains of *P. patulum.*

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family
Acacia senegal gum acacia gum arabic tree	senegal gum comprised chiefly of salts of: calcium, potassium, magnesium	Pea or bean (Fabaceae)

Early Egyptians valued gum arabic for treating dysentery, sore nipples, inflammations, burns, gonorrhea, and nodular leprosy; it figured prominently in commerce. Today it is commonly used as a demulcent ingredient in pharmaceuticals for treating dysentery, diarrhea, coughs, fever, and throat irritations; and as a binding agent in tablets and pills, especially lozenges and cough drops.

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family
Aloe barbadensis Mediterranean aloe *Aloe ferox* Cape aloe *Aloe perryi* Zanzibar aloe	anthraquinone glycosides (aloin) including: barbaloin (which yields aloe-emodin, a purgative)	Lily (Liliaceae)

During the time of Alexander the Great, *Aloe* was cultivated for use as a purgative. In folk medicine, it has often been used for inflammations of the skin and eyes, and for sores, minor cuts, and burns. In 1935 its efficacy against x-ray burns was demonstrated. In modern-times aloin extracts and powdered *Aloe* latex have also been used as a purgative, especially for chronic constipation. Today it is used mainly as an ingredient in tincture of benzoin, which capitalizes on its antibacterial and skin-healing properties.

Species and Common Name	Active Ingredients	Family
Atropa acuminata Indian belladonna *Atropa belladonna* English belladonna; deadly nightshade	Alkaloids, including: hyosyamine (both spp) atropine hyoscine (scopolamine)	Nightshade or Potato (Solanaceae)

In classical times, belladonna was employed as a poison, and its hallucinogenic properties were associated with magical and mystical practices. It was also used as a sedative and nerve tranquilizer. Today leaf preparations serve as relaxants, sedatives, and anodynes; they are antidiuretic and antiasthmatic. Leaf extracts are also used in ophthalmology, and for the treatment of Parkinson's disease, epilepsy, convulsions, whooping cough, night sweats, kidney and gallbladder stones, and gastric ulcers. Where root preparations are official, they are used for gout and rheumatism.

Species and Common Name	Active Ingredients	Family
Cassia angustifolia Indian or mecca senna *Cassia senna* Alexandrian or Nubian senna	glycosides, including sennosides A,B,C, and D	Pea or bean (Fabaceae)

Senna was first introduced to European medicine by Arabs in the 9th and 10th century. A leaf infusion is used in India, Pakistan, and Iran as a laxative, and a paste of powdered leaves is used for eruptions and skin diseases. In Africa it is used as a purge to allay fever, and the leaves are used on burns and wounds. Commercially, it is used to formulate laxatives, and extracts are made from both leaves and pods. Pure extracts of sennosides A and B were highly effective in treating severe constipation in Finland.

Species and Common Name	Active Ingredients	Family
Cephaelis ipecacuanha Brazilian ipecac golden root	isoquinoline alkaloids (from roots and rhizomes) including: emetine, cephaeline	Madder (coffee) (Rubiaceae)

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family

Brazilian Indians have traditionally used ipecac for dysentery. It was introduced to Europeans in the 15th century and was widely employed for dysentery from the 17th to the 19th century. Now we use injections of emetine preparations to treat amoebic dysentery. In India it has been used successfully against bilharziasis, oriental sores, and Guinea worms. One of its most widespread uses is to induce vomiting in cases of poisoning.

Species and Common Name	Active Ingredients	Family
Cinchona calisaya *Cinchona ledgeriana* Other *Cinchona* spp. quinine Peruvian bark	alkaloids: quinine	Madder or Coffee (Rubiaceae)

Cinchona bark was prized by South American Indians as a cure for fevers and malaria. It became known to the Spaniards in the early 1600's. Quinine has been an important antimalarial drug since that time until the development and widespread use of synthetic substitutes. It was used for U.S. troops, however, during both World War II and the Indochina war. It is principally cultivated today as a source of quinidine—an antiarrhythmic drug for regulating heartbeat.

Species and Common Name	Active Ingredients	Family
Colchicum autumnale autumn crocus meadow saffron	colchicine and other alkaloids	Lily (Liliaceae)

The ancient Romans and Greeks treated rheumatism, gout, arthritis, dropsy, enlarged prostate, and gonorrhea with the corms and seeds. Now we administer colchicine (orally) for gouty arthritis. In Egypt colchicine successfully treats familiar Mediterranean fever. It cannot be artificially synthesized cheaply.

Species and Common Name	Active Ingredients	Family
Digitalis lanata Grecian foxglove wooly foxglove	digoxin lantoside C	Figwort (Scrophulariaceae)
Digitalis purpurea purple foxglove	digitoxin gitoxin	

Europeans have used digitalis since before the 10th century, first against epilepsy, sore throat, and as an expectorant; in 1775, for dropsy; and by 1877 as a cardiac sedative, cardiotonic, and a diuretic. Today we treat congestive heart failure with digitalis preparations. It increases the strength of systolic contractions and lengthens the rest period between contractions. It is most effective against hypertensive heart disease, low blood pressure, and dilated hearts. It serves as a diuretic, reduces edema, and improves circulation.

Species and Common Name	Active Ingredients	Family
Dioscorea composita Mexican yam; barbasco *Dioscorea floribunda* alambrillo Other *Dioscorea* spp.	saponin glycosides for conversion to steriodal sapogenins (diosgenin)	Yam (Dioscoreaceae)

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):		
Species and Common Name	**Active Ingredients**	**Family**

Plant saponins are foaming agents which have historically been utilized as detergents, e.g., Dioscorea deltoides is a traditional laundering agent used on raw wool and woolen fabrics in the western Himalayas. However, the Meskwaki people use tea prepared from the tubers of *D. villosa* to relieve the pain of childbirth. The use of *Dioscorea* saponins for making contraceptives is basically a modern phenomenon though; in addition to oral contraceptives, other common steriod drugs include cortisone and hydrocortisone, which are used for arthritis, skin diseases, and Addison's disease.

Duboisia myoporoides corkwood "eye-plant"	leaves contain tropane alkaloids especially: hyoscine, (scopolamine) and hyoscyamine (in both)	Nightshade (Potato) (Solanaceae)
Duboisia leichhardtii Leichhardt corkwood	atropine	

Extracts have been used in Europe and Australia since 1877 in opthalmology to dilate the pupil. It has also been used for goiter, mania (delirium), and bladder inflammations, and as a sedative for corneal inflammations. Atropine derived from hyoscyamine extraction is still the most economically efficient means of producing this drug. Hyoscine was widely used during World War II for motion and seasickness, and is still employed today.

Ephedra major and other *Ephedra* spp. joint fir	The alkaloids: ephedrine pseudoephedrine (isoephedrine)	Ephedra (Ephedraceae)

The Chinese have used *Ephedra* for over 5,000 years in pills and herbal teas for treatment of colds, coughs, headaches, infectious eruptions and malarial and other fevers. Today ephedrine is used for asthma, emphysema, hay fever, and rhinitis; it is also used to treat nocturnal enuresis and some types of epilepsy. Salts of it are used in nasal sprays for relief of swelling and congestion. Pseudoephedrine is effective in alleviating nasal congestion when taken orally.

Erythroxylum coca coca bush cocaine plant or tree	cocaine (alkaloid)	Coca (Erythroxylaceae)

Coca leaf infusions have long been used in South America as a sedative (for nerves), a sudorific, a stomachic, and a remedy for asthma. Andean Indians still rely on it as a stimulant and hunger depressant. It is chewed or smoked for colds, catarrh, and asthma. First isolated in 1858, cocaine was finally employed in 1884 as a local anesthetic; today it is used in nasal and oral operations or for inoperable cancer. It is also indicated for earaches, and used as an ingredient in suppositories and ointments for relief of hemorrhoids and neuralgia.

Glycyrrhiza glabra licorice sweet wood	glycyrrhizin and other glycosides	Pea or bean (Fabaceae)

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family

Root decoctions have long been used for coughs, bronchitis, catarrh, laryngitis, and sore throat. Its anti-inflammatory properties were employed in European medicine for alleviating inflamed stomachs and indigestion; it has been given to desert troops to prevent extreme thirst or for low water intake. In India, it has been applied to cuts and wounds. Today licorice extracts are used in cough syrups and drops, and are sometimes prescribed for duodenal and gastric ulcers. Licorice may also be beneficial for treatment of dermatitis, Addison's disease, and rheumatoid arthritis. Glycyrrhizin is now known to induce sodium retention, and it inreases extracellular fluid, actions which aid in retention of water.

Juniperus oxycedrus prickly cedar sharp cedar	cade oil or juniper tar oil, which includes *d*-cadinene	Cypress (Cupressaceae)

Ancient uses of cade oil include treatment of corneal opacities, pain due to dental caries, head lice, snakebite, and leprosy. It has long been used to treat parasitic skin diseases and to promote healing of wounds. Today cade oil is used in ointments, creams, and pastes for treatment of parasitic skin diseases, pruritic dermatoses, and eczema. It is also used in shampoos for seborrheic dermatitis, and in antiseptic soaps.

Mentha arvensis subsp. *haplocalyx* Japanese mint corn mint	menthol	Mint (Lamiaceae)

In Japan this plant has historically been employed as a home remedy for coughs and colds. Now it is used throughout the world in nasal inhalants and cough drops; since it is antiseptic, anaesthetic, and soothes sensitive or irritated skin, *Mentha* is an ingredient in lotions and creams or ointments to treat skin diseases.

Myroxylon balsamum var. *pereirae* Peruvian balsam Indian balsam	benzoic acid benzyl cinnamate benzyl benzoate resins	Pea or bean (Fabaceae)

In Central America and southern Mexico, the people employ a leaf decoction as a vermifuge (to expel worms) and as a diuretic. It has long been used there to heal cuts and wounds, and to treat gonorrhea, rheumatism, asthma, and catarrh. In Guatemala it is sold in native markets for relief of itch. Since balsam is bactericidal it has been widely employed for syphilitic sores and other ulcerous conditions; it is employed today in ointments as an antiseptic, parasiticide, and fungicide, especially, for ringworm, scabies, pediculosis, wounds, bed sores, ulcerations, chilblains, diaper rash, and to relieve the itch of hemorrhoids and anal pruritus.

Papaver bracteatum great scarlet poppy	papaverine morphine, codeine, noscapine thebaine (from both spp.)	Poppy (Papaveraceae)

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family
Papaver somniferum opium or white poppy		

Ancient uses of the Opium poppy date back before the 3rd century B.C. It was valued by the Romans, Greeks, and Arabs for sedative potions, and by the Chinese for curing dysentery as well. Opium preparations were in common household use in the U.S. to induce relaxation, allay pain, and calm nerves (until the last century). In India today a decoction of the capsules is used for painful swellings and inflammations. In Mohammedan medicine it was traditionally used for coughs, dysentery, diarrhea, and asthma. In the United States, morphine sulfate is currently used to alleviate pain due to terminal cancer and other instances of severe pain, for internal hemorrhages, traumatic shock, and typhoid fever. Codeine sulfate or phosphate is used as an analgesic and in cases of persistent coughs. Noscapine is an antitussive, and papaverine reduces vasospasms in cases of arterial embolism or spasms of gastric or intestinal linings. Thebaine is primarily converted to codeine; it is also the source of Naloxone, a life-saving drug given to infants of heroin addicts.

Plantago ovata Indian plantago blond psyllium	seeds yield a colloidal mucilage	Plantain (Plantaginaceae)
Plantago psyllium black psyllium French or Spanish psyllium		

Added to the Indian Pharmacopoeia in 1868, psyllium seeds were used as a demulcent and for relief of constipation, the mucilage acting as a lubricant and toxin-absorbing agent. It also overcomes dysentery and diarrhea. Powdered psyllium seeds are a common ingredient in laxative preparations provided by many U.S. manufacturers. A solution of salts of liquid fatty acids known as Sodium Psylliate Injection is also given as a sclerosing agent.

Podophyllum peltatum May apple	podophyllin (podophyllum resin) which includes lignin glycosides such as podophyllotoxin	May apple (Podophyllaceae)

American Indians used drops of fresh rhizomes to relieve deafness and as an emetic. Penobscot Indians used it for venereal warts. In 1864, powdered podophyllin was used for syphilis, gonorrhea, kidney, prostate and bladder problems, dysentery, chronic hepatitis, constipation, and typhoid fever. Today podophyllin is employed as a cathartic; it is combined with milder laxatives for chronic constipation. Podophyllin resin with tincture of benzoin is used effectively on venereal warts, plantar warts, and in veterinary medicine. Podophyllin ointments are also sometimes used on lesions (hypertrophic and hyperkeratotic). Study of this species has led to the discovery of potentially useful anticancer compounds in a related species, *P. emodi* of India.

Rauvolfia serpentina serpent wood Other *Rauvolfia* spp.	alkaloids, including: reserpine rescinnamine deserpidine	Dogbane (Apocynaceae)

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):		
Species and Common Name	**Active Ingredients**	**Family**

For 4,000 years *Rauvolfia* has been used in India for snakebites, insect stings, epilepsy, nervous disorders, mania, dysentery, diarrhea, cholera, fever, worms, and to promote uterine contractions during childbirth. In 1949 reserpine was reported as the best hypotensive drug compound available. Since 1953 it has been used as a tranquilizer and to treat mild hypertension, anxiety, schizophrenia, menopausal disturbances, and menstrual tension. It cannot be synthesized cheaply enough to displace the natural product.

Species and Common Name	Active Ingredients	Family
Ricinus communis castor bean castor oil plant	castor oil, which contains ricinolein (a purgative) and glycerides; ricin	Spurge (Euphorbiaceae)

Ancient Egyptians mixed castor oil with their beer and used it as their standard laxative. It has long been cultivated pantropically for various folk remedies, including headaches, fevers, rheumatism, inflamed muscles, lumbago, and sciatica. It is widely used in eye drop preparations and opthalmic medications, skin diseases, and on wounds of animals; it has been used with turpentine to expel tapeworms. In earlier years castor oil was the universal household purgative; today it is used primarily in hospitals as a laxative prior to x-rays or examinations, and for cases of food poisoning. The oil is also used to make contraceptive creams, jellies and foams, and undecylenic acid, an antifungal compound. The highly toxic compound ricin has recently shown promise for treating leukemia when used in combination with antibody therapy.

Species and Common Name	Active Ingredients	Family
Strophanthus gratus smooth strophanthus	cardiac glycosides, especially ouabain (G-strophanthin)	Dogbane (Apocynaceae)
Strophanthus kombé green strophanthus	K-strophanthin	

In Nigeria, extracts of crushed stems are administered as a folk medicine for extreme debility, and leaf preparations are used for fever and as a remdy for gonorrhea. In Africa, *S. kombé* root preparations are used for bronchitis, and a seed gum is used as an arrow poison that paralyzes the heart. Ouabain is used as a cardiac stimulant in the United States, England, and other countries; it acts more quickly than other cardiac stimulants; it is especially valued for emergency treatment of acute heart failure, and to treat hypotension during surgery. K-strophanthoside from *S. kombé* was once used in cases of pulmonary edema.

Species and Common Name	Active Ingredients	Family
Styrax benzoin Sumatra benzoin benzoin tree	fresh benzoin resin contains: benzoic or cinnamic acids	Storax (Styracaceae)
Styrax tonkinese Siam benzoin		

Benzoin has historically been used by the Malay people to heal sores on feet and circumcision wounds, and to relieve shingles, ringworm, and other skin afflictions. In other areas people have used it to heal cracked nipples. It was given and traded to European explorers in the 15th and 16th centuries. Today benzoin is the most important ingredient in compound tincture of benzoin (friar's balsam). This compound is used as an antiseptic, for ulcers, on facial fever blisters or

TABLE 1. (Continued)

VASCULAR PLANTS (Division Tracheophyta):

Species and Common Name	Active Ingredients	Family
cold sores, and on blistered or cracked skin. It is also painted onto body surfaces to aid in adhesion of dressings and adhesive tapes. Used internally, it is an expectorant, diuretic and carminative. A vapor of it is inhaled for bronchitis or laryngitis.		
Thymus vulgaris common or garden thyme	thymol	Mint (Lamiaceae)
Thymus zygis wood marjoram	carvacrol	
In the classical era, thyme was valued as a fumigating herb and antiseptic. It was once widely employed as a sudorific and remedy for coughs. Since the 16th century thyme oil (from *T. zygis*) has been used in disinfectants and as a germicidal agent, particularly in gargles, mouthwashes, dentrifices, and cough drops. Modern investigations have demonstrated that thyme oil is effective against *Salmonella, Streptococcus, Staphylococcus,* and other bacteria; two thyme extracts were isolated in Italy, one effective against gram-positive bacteria and the other against gram-negative bacteria. Thymol is used to treat fungus diseases of the skin, and sometimes is used as an antiseptic for wounds and sores.		
Veratrum viride American hellebore green hellebore	ester alkaloids, including: germidine, germitrine, and glucosides of these alkamines	Lily (Liliaceae)
Veratrum album white hellebore		
This plant was used for curative purposes by American pioneers and Indians. It was an important analgesic for painful diseases in the 18th and 19th centuries; it was used as a cardiac sedative or for treatment of convulsions, epilepsy, and pneumonia. An alkaloid mixture or powdered rhizome may be utilized for treatment of hypertension, sometimes in combination with *Rauvolfia* alkaloids. Now it is usually employed in emergency situations, e.g., hypertensive toxemia (during pregnancy) or pulmonary edema.		

Sources: Morton, 1977; Lewis and Lewis, 1977; Schery, 1972.

Peoria, Illinois. A much more productive species, *P. chrysogenum* has served as the parent material for selection of the high-yielding *Penicillium* strains which now produce nearly all of the world's penicillin. And ever since the 1940's, penicillin and its more recent derivatives have been worth millions of dollars annually to the pharmaceutical industry.

Just as in the case of our important medicinal compounds obtained from fungi, e.g., the ergot alkaloids and penicillin and its derivatives, most of the plant drug compounds used in modern pharmaceutical preparations are extracted from species that have a long history of folkloric use. For example, the red seaweed (*Digenea simplex*) is an ancient Japanese folk remedy used for expulsion of worms; modern studies of this red sea alga resulted in the isolation of kainic acid, an unusual amino acid now available commercially as an anthelmintic. Other examples include products from the more taxonomically advanced gymnosperms (cone-bearing plants);

Fig. 1. Ergot *(Claviceps purpurea)* (arrows) infecting rye plants. (Photo: Agricultural Research Service, USDA)

Fig. 2. Three, fused penicillin *(Penicillium chrysogenum)* colonies. (Photo: USDA)

cade or juniper tar oil from the prickly cedar (*Juniperus oxycedrus*) is still valued for treatment of parasitic skin diseases, while the ephedra alkaloids from *Ephedra major* and other species are still used in preparations for coughs, colds, and nasal or bronchial congestion.

Serpent-wood (*Rauvolfia* spp.) provides an excellent example of a higher plant species that has yielded medicinal compounds useful for treating an affliction of modern man as well as some of humanity's age-old ailments. Although at least four tropical serpent-wood species are now used commercially, the Indian species (*R. serpentina*) was the one first encountered by the Western world. A native of the tropical forests of East India, this drug plant has long been used in ancient Indian folk remedies for treating mental and nervous disorders, dysentery, diarrhea, fevers, insect stings, and snakebites, as well as other sources of physical stress. Yet it was not recognized as a valuable medicinal plant by Western scientists until the 1940's, and the anti hypertensive alkaloid reserpine was not isolated chemically and marketed in the United States until the early 1950's. Today, rauwolfia alkaloids obtained from serpent-wood root extracts are used for many of the same human afflictions for

which rauwolfia whole root was used in the past. Additionally, reserpine is used as a tranquilizer in cases of insanity and as a treatment for dysentery, fevers, and insect stings. However, in modern medical practice, the principal use of reserpine and other rauwolfia alkaloids is for treatment of hypertension, a health problem that has become prevalent in modern industrialized societies. In recent years, most antihypertensive drugs sold in U.S. pharmacies (excluding hospitals) have contained products derived from serpent-wood root extracts. The most commonly used antihypertensive alkaloid, reserpine, was present in 1.5 percent of all 1973 U.S. community prescriptions. Since the 1950's and the chemical isolation of reserpine, demand for *R. serpentina* roots became so intense that it resulted in the virtual extermination of most of the wild stands in India and Java. Thus, as early as 1954, large-scale collection of the African species, *R. vomitoria,* was initiated in the Congo. And when commercial supplies of Indian serpent-wood were cut off in 1955, another suitable substitute species, American serpent-wood (*R. tetraphylla* or *R. canescens*), was located in the tropical forests of Central America. Today the international market is served primarily by wild stands of the African species, while both wild and cultivated stands of *R. serpentina* in India produce only about 30 tons of dried roots for local consumption. In addition to the use of rauwolfia root extracts, alkaloids from rhizome extracts of two temperate hellebore species (*Veratrum viride* and *V. album*) are used alone or in combination with rauwolfia root alkaloids for treatment of hypertension. In 1967, almost 90 percent of the U.S. prescription drugs used as antihypertensives were ultimately derived from *Rauvolfia* or *Veratrum* species.

Heart disease and heart failure are currently leading causes of death in the United States. In addition to the great value of plant compounds as antihypertensive drugs in our country, more than 85 percent of the 1967 community prescriptions of miscellaneous cardiovascular drugs were also derived from higher plant extracts. This amounted to 2.25 percent of all U.S. prescriptions that year. Most of the miscellaneous cardiovascular drugs (98 percent) were either cardiotonic or antiarrhythmic drugs obtained from two genera of flowering plants—foxglove (*Digitalis*) and quinine (*Cinchona*). Cardiotonic drugs are used as cardiac stimulants for treatment of congestive heart failure; if the latter is precipitated by hypertension or atherosclerosis, cardiac glycosides from *Digitalis* usually produce the best results. It has been estimated that about 3 million sufferers from heart failure in the United States routinely use digoxin—a drug obtained from the Grecian or wooly foxglove (*Digitalis lanata*) of central and southern Europe. Other cardiotonic drugs are also obtained from this species as well as the purple foxglove (*D. purpurea*) (Fig. 3). Additionally, strophanthus species (*Strophanthus gratus* and *S. kombé*) are our principal sources of ouabain and K-strophanthin. Ouabain is particularly valued as a cardiac stimulant as well as for emergency treatment of heart failure since it is very rapidly absorbed and is thus faster acting than digoxin and other cardiotonics.

In contrast to stimulative effects of cardiotonic drugs, antiarrhythmic drugs are used to control or manage cardiac arrhythmias or erratic and irregular heartbeat. Digoxin and lanatoside C, both from Grecian foxglove, are used for acute arrhythmias since they are rapidly absorbed, fast-acting, and quickly eliminated from the body. However, ouabain is sometimes used instead when an even more rapid onset is required. In addition, quinidine (from the bark of quinine trees) is a relatively new drug employed for regulation of heartbeat. The bark of *Cinchona ledgeriana,* once widely harvested and cultivated for quinine—our most ancient antimalarial

Fig. 3. A temperate Old World species, purple foxglove *(Digitalis purpurea)* has also become familiar to many North American gardeners who value it as an ornamental. (Photo: Agricultural Research Service, USDA)

drug—is now cultivated primarily as a source of quinidine. The latter drug was accidentally discovered when malaria patients treated with quinine bark were found to be free of cardiac arrhythmias. Although such new uses of drug plants can be discovered in this way, i.e., through use of whole plant extracts, ancient or folkloric uses of plants usually provide more clues about useful drug compounds. For example, medicinal use of foxglove was recorded in 1250 and can be traced back before the 10th century. But even though foxglove is listed in the well known European herbals of early times, its value for treating heart afflictions was not known in established medical practice until the late 18th and early 19th centuries. In 1775 an English medical doctor, William Withering, first proclaimed the effectiveness of digitalis as a diuretic and treatment for dropsy—fluid accumulation (edema) now known to be

brought on by heart disease. Withering learned of the dropsy-relieving effects of digitalis leaf preparations from a Shropshire woman; actually, many other illiterate housewives and farmers in England and Europe had used digitalis for centuries for relief of dropsy. Withering worked for many years to establish the relationship between dropsy and heart disease through his studies of the effects of digitalis preparations on afflicted patients.

Saponin-containing *Dioscorea* species (related to the edible, tropical yams which lack saponins) contribute the drug precursors for approximately 95 percent of our hormonal drugs—the second largest category of therapeutic drugs (next to antibiotics). Natural sources of steroids were present in about 225 million prescriptions dispensed from U.S. pharmacies in 1973, or more than 14.5 percent of all community drug sales. The major hormone drug categories include topical hormones and corticosteroids, e.g., cortisone, hydrocortisone; oral contraceptives, e.g., norethindrone preparations such as Norinyl and Ortho-Novum; anabolic agents; and sex hormones (androgens, estrogens, and progestogens). The use of steroid drugs is a recent phenomenon in medical practice. Although the medical value of sex hormones and corticosteroids was widely apparent by the 1940's, the cost of extracting and purifying them from animal sources severely curtailed their availability before the discovery of dioscorea saponin glycosides. Extract yields from animal glands were found to be extremely low, thus making the hormonal compounds very costly (around $200 per gram). For example in the 1930's, only 12 mg of estradiol—a female sex hormone—was extracted from 4 tons of sow ovaries (80,000 animals), while about 15,000 liters of male urine was required to produce only 15 mg of androsterone. Similarly, although many plant species are known to produce steroidal precursors and some, e.g., *Strophanthus* spp., *Agave sisalana,* and soybeans (*Glycine max*), were used commercially before *Dioscorea,* their yields of the necessary raw starting materials were relatively low. Thus, the discovery of abundant wild stands of Mexican yams which produce good quantities of diosgenin was fortunate for the pharmaceutical industry. Of the 125 *Dioscorea* species that have been evaluated for diosgenin production, two tropical Mexican species, *D. composita* and *D. floribunda,* have proved to be the best commercial sources.

Ever since the successful establishment of the Mexican steroid industry in the late 1940's by the American organic chemist Russell Marker, the supply of hormone drugs has increased while their cost has declined significantly. Marker, one of the first chemists to discover the potential usefulness of plant sapogenins, was unable to interest the American drug firm which sponsored his initial research in his idea of a Mexican industry. So he struck out on his own and began to manufacture progesterone from diosgenin extracted from wild dioscorea tubers harvested from Mexican jungles. For many years, Mexico produced virtually all of the diosgenin used for the semisynthetic production of steroids. However, overharvesting of wild stands in many parts of Mexico began to exhaust commercial sources of dioscorea tubers. Gradually, wild stands of *D. floribunda* in Guatemala and other species in Puerto Rico, India, and China were also employed to meet the growing demand for steroids. Presently, world consumption is estimated at between 1,270 and 1,380 tons of diosgenin equivalent, about half of which is still obtained primarily from wild plants in Mexico. However, since the availability of wild Mexican yams has steadily declined and prices set by the Mexican government have greatly increased its cost to industrial producers, the gap has begun to be filled by alternative plant raw materials

converted to steroids by microbial fermentation processes. High costs associated with dioscorea cultivation and the possibility of developing cost-competitive, total synthetic processes have inhibited the establishment of large-scale cultivation operations. Even though there may be a shortage of needed plant steroidal precursors within the near future (estimated demand for 1985 is around 2,400 tons of diosgenin equivalent), the new semisynthetic and synthetic processes for steroid production have already become firmly established. However, the steroid industry would not be where it is today without these tropical Mexican yams. Even though the discovery of these valuable medicinal plants has been fortunate for mankind, it is most unfortunate that this social and industrial progress has been attained at the expense of many wild dioscorea populations. If cultivation of dioscorea is deemed worthwhile or necessary in the future, it is possible that we have already sacrificed and forever lost some of the best high-yielding or disease-resistant germplasm resources.

A great variety of other plant species used for medicinal purposes in the past are still used in modern pharmaceutical preparations. For example, belladonna or deadly nightshade (*Atropa belladonna*) (Fig. 4) is a toxic European ornamental and drug plant that has been used as a poison since classical times. But its sedative and other beneficial effects were well known to European herbalists long before belladonna ex-

Fig. 4. Belladonna or the deadly nightshade *(Atropa belladonna).* Belladonna is the source of the medicinal alkaloids—atropine and *l*-hyoscyamine. Although this species is no longer used officially for medicinal purposes in the United States, a related species, Indian belladonna *(A. acuminata),* is used pharmacologically in sedatives, relaxants, and anti-asthmatic preparations. Belladonna extracts are also used to treat certain nervous disorders. (Photo: Agricultural Research Service, USDA)

tracts were officially introduced into the British and U.S. pharmacopoeias in the early 19th century. Today leaf extracts from belladonna and a related species, Indian belladonna *(A. acuminata)*, are used in sedatives, relaxants, antispasmodics, and antidiuretics; and they are employed in drugs for treating asthma, epilepsy, Parkinson's disease, gastric ulcers, kidney or gall stones, whooping cough, and overdoses from depressant poisons such as opium. In 1973, almost 10.5 million community drug prescriptions (0.67 percent of all) contained belladonna extracts. In addition, most of the synthetic, antispasmodic drugs on the market today were modeled after the chemical structure of tropane alkaloids (atropine, scopolamine, and hyoscyamine) derived from belladonna and other solanaceous plants (henbane and corkwood species). Similarly, opiates from the opium poppy (*Papaver somniferum*) are ancient painkillers that are still valuable analgesics today; more than 2 percent of 1973 U.S. prescriptions contained codeine or morphine derived from this species. Annual legal imports of opium to the United States have averaged 158,730 kg (350,000 lb) in recent years. In addition to relieving pain, codeine is often used in cough suppressants, as is ephedrine, an alkaloid from *Ephedra* species. *Ephedra* has been used in herbal teas and pills in China for over 5,000 years for relief of nasal or bronchial congestion due to coughs, colds, and asthma.

Animal and Bacterial Products

A number of animal species also provide valuable sources of medicinal compounds. For example, hormone drugs derived from animals were present in 32.8 million U.S. prescriptions in 1967. These accounted for approximately 67 percent of all such pharmaceuticals containing animal substances. Animal-derived extractives are commonly obtained from the organs or glands of healthy, domesticated animals. For example, thyroid products are obtained from the thyroid glands of hogs and sheep, and until very recently, insulin was obtained primarily from the pancreas of hogs and oxen. Other common products derived from familiar animals include the conjugated estrogens (primarily from the urine of pregnant mares), epinephrine, oxytocin, bile acids, and a variety of digestive and other enzymes. Although wild terrestrial animals have yet to be extensively studied as sources of drugs, many of them already have established pharmaceutical potential. For example, a steroidal constituent obtained from toad (*Bufo* spp.) poison, resibufogenin, is now in clinical use in Japan as a respiratory stimulant. A similar toad poison extract, bufalin, exhibits cardiac activity equivalent to a digitoxin derivative of *Digitalis purpurea;* it is also 90 times as potent as cocaine as a local anesthetic. It is interesting that of the 50 or so steroidal compounds that have been recently characterized from toad poisons (by 1970), the majority of the species from which they were obtained are listed in the Ch'an Su, a Chinese medical treatise written in 1596. Toad poison compounds have been traditionally valued in Chinese medicine for their cardiac, anesthetic, and anti-inflammatory effects. Moreover, powdered toad skin was a highly recommended treatment for congestive heart failure and difficult breathing, as noted in several European pharmaceuticals written during the 15th to early 18th centuries.

In addition to medicinals derived from terrestrial animals, many drugs or drug compounds are extracted from marine fauna. Although exploration of the oceans for useful pharmaceutical substances is a relatively recent activity, some marine products have been used medicinally for a very long time. One well known product is

fishliver oil; for example, codliver oil is commonly used in vitamin A and D therapy. It is also the major ingredient in a soothing ointment used for diaper rash, chafing, and other minor skin irritations. In contrast, many novel pharmaceuticals have been obtained from marine animals during the last few decades. One new drug, Ara-A (adenine arabinoside), has proven useful for treatment of pinkeye (keratoconjunctivitis) and other virally induced eye infections or inflammations such as those caused by *Herpes simplex* viruses. Ara-A is one of the few drugs ever licensed by the U.S. Food and Drug Administration for treating viral diseases. It has also been effective in reducing deaths caused by herpes encephalitis, an unusual type of brain inflammation that commonly results in damage to the central nervous system even if the patient survives. In a pilot study conducted at 15 medical centers, Ara-A therapy reduced herpes encephalitis mortality from 70 to 28 percent. This antiviral drug was obtained via study of a Caribbean sea sponge, *Cryptotethya crypta,* in the late 1940's. It was initially examined for anticancer activity (see Table 3), and its viricidal properties were accidentally discovered in the 1960's.

Other novel drugs from marine organisms include tetrodotoxin and pralidoxime chloride. Tetrodotoxin, 160,000 times as potent as cocaine for blocking nerve impulses, is currently used in Japanese clinics as a local anesthetic and muscle relaxant for terminal cancer and neurogenic leprosy patients. This drug compound has been extracted from certain puffer fish, porcupine fish, and ocean sunfish; it has also been isolated from a California newt, a goby from Taiwan, and some Central American frog species. Pralidoxime chloride was also developed in Japan, but it is now an approved drug in the United States for treating victims of pesticide and organophosphate chemical poisonings. Pralidoxime is particularly valued in Japan where frequent cases of organophosphate insecticide poisonings have occurred from ingestion of contaminated rice. The number of marine drugs that has been recently developed in Japan is not surprising considering the long history of association of these people with the marine environment, and the great variety of sea life forms used in Japanese folk medicine. Recent research by scientists from the United States and other nations has uncovered a wealth of other toxic compounds from poisonous sea animals that possess antimicrobial, antiviral, cardioactive, and neurophysiologic properties. Many of these substances possess chemical structures unlike those found in any terrestrial species. Thus by continuing our search of the seas as well as land, we can discover a variety of novel drug substances.

In addition to drugs from "higher" animals, certain pharmaceuticals are still derived directly or indirectly from microbes. The primary contribution of microbial drugs is their role in the development of antibiotics, the largest therapeutic drug category. Among the families of the true bacteria, only members of the *Bacillus* family (Bacillaceae) have yielded useful antibiotics. Examples of those produced by various *Bacillus* species include bactricin, gramicidin, and the polymyxins. However, *Streptomyces* bacteria of the actinomycetes have been by far the most important sources; examples include such well known drugs as the tetracyclines, oxytetracyclines, aureomycins, neomycin, Kanamycin, actinomycins, and nystatin. Streptomycin, isolated from a *Streptomyces griseus* culture in 1943, was the first bacterial antibiotic to be marketed in the United States; within only three years after its discovery, annual sales had surpassed $50 million. The production of such bacteria-derived pharmaceuticals has been a multi-million dollar business ever since World War II. Recently 58 percent of the antibiotics derived from natural sources

have been obtained from *Streptomyces* species, with an additional 9 percent from other bacteria. Other natural antibiotic sources include the lower plants (mosses and algae), fungi and lichens (19 percent), and higher plants (14 percent).

Although some antibiotics can be produced more cheaply by artificial synthesis, it is usually more practical to use the biological machinery of the bacteria for production. In any case, provision of chemical models of compounds originally isolated from microorganisms is a necessary first step for industrial synthesis of antibiotics. For example, the synthetic drug metronidazole, used for treatment of trichomoniasis and amoebic dysentery, was modeled after the microbe-derived antibiotic azomycin which is not used clinically. In addition to antibiotic production, vitamins, vaccines, diagnostic agents, enzymes, and some medicinal alkaloids are also manufactured directly or indirectly by employment of microorganisms.

Economic Value of Medicinal Biota in the United States

In addition to the direct, health-restoring benefits obtained from naturally derived pharmaceuticals, medicinal biota contribute significantly to the economic productivity of the United States and other nations. As discussed previously, in the United States alone the retail value of all legally dispensed prescription drugs containing natural ingredients was recently estimated at $3 billion. However, this figure does not include the value of the multimillion dollar medicinal herb trade, nor does it reflect the annual export value of medicinal biota to the U.S. economy. More than 125 species of flowering plants are still collected from the wild within the Appalachian region alone. Examples include lobelia (*Lobelia inflata*) which is the source of the alkaloid lobeline used as an antispasmodic, emetic, and ingredient in anti-smoking pills; it is related to 5 species and 2 subspecies of Hawaiian lobelias currently threatened with extinction. And goldenseal (*Hydrastis canadensis*) has diuretic properties, and has long been used as both a tonic and a treatment for mouth ulcers. It is now considered threatened in possibly as many as 23 states.

Collection and sale of wild medicinal plant products is a significant source of income for many people living in the Appalachian Mountains and other parts of the United States. Moreover, beneficial or curative properties have been frequently experienced with use of fresh herbs, whole plant extracts, or combinations of herbs, even though processed extracts or pills derived from the same plants have often been judged ineffective. When used properly, many medicinal herbs can be employed as health restorative aids. However, like most medicinal biota, they often contain toxic or poisonous compounds. They must be used knowledgeably and with extreme caution since improper use can result in accidental poisoning or death. In addition, commercial exploitation has brought some species or distinct populations to the brink of extinction. Examples include the U.S. medicinal herbs *Echinacea tennesseensis,* a coneflower which yields echinacea roots, and threatened populations of goldenseal. Probably the most well known, threatened U.S. medicinal plant is American ginseng, (*Panax quinquifolium*) (Fig. 5), of our native northern deciduous forests:

> . . . Ginseng is the only plant used routinely by so great a number of more or less healthy individuals for stimulation, added energy, and a sense of well-being—a panacea for the healthy who want to remain well for a long time and if possible become healthier (Lewis and Lewis, 1972, p. 382).

Widespread belief in the curative powers of ginseng still prevails in China, where it has been used for centuries. Although American ginseng is currently of little com-

Fig. 5. The branch, cluster of berries, flower, seeds, and root of American ginseng *(Panax quinquifolium)*. Both wild and cultivated U.S. ginseng plants have been harvested for their leaves and valuable roots—primarily for export to China. (Illustration: Agricultural Research Service, USDA)

mercial value in the United States, it has been commonly exported to China for huge profits for centuries. The ginseng trade increased tremendously within the last few decades. In 1972-1973, U.S. exports amounted to $8,900,000, whereas a decade before they averaged only $2.7 million annually; 1976 estimates placed exports at about $15 million.

Extraction of ginseng for commercial sale has proceeded primarily at the expense of wild populations, many of which were exterminated or severely depleted throughout the northeastern woodlands where they once thrived (before ginseng was brought into large-scale cultivation). American ginseng is now listed on Appendix II of CITES for purposes of international trade. This allows trade in the wild roots to be monitored. In recent years about two thirds of all exports have been comprised of roots derived from cultivated plantings. The depletion and extinction of gene pool resources of *Panax quinquifolium* in the United States provides an example of the consequences of economic overexploitation of a useful medicinal species. In such cases, too little regard is shown either for the breeding populations—the "breeding stock" for the species—or for long-term (*in situ*) conservation and protection of their essential habitats.

Indirect Uses of Medicinal Gene Resources

In addition to their direct health and economic benefits, medicinal gene resources are also used for biomedical research or as evaluative or investigative tools for drug testing and development. Although the term medicinal biota may seem more appropriate, it should be remembered that the usefulness of these species typically results from the activity of alkaloids or other chemical compounds produced ultimately by gene action. Moreover, the value of vertebrate animals as experimental subjects, particularly the nonhuman primates, is based on similarities that exist between their systems and those of humans. And the physiological, biochemical, or other traits of each species are determined by its own, unique genetic constitution.

A great variety of animals, plants, and microbes are essential components of the drug development and testing process. Tetrodotoxin, the drug compound obtained from certain marine fish and terrestrial amphibians, is such a potent agent for blocking nerve impulses that it has also been used for the study of nerve impulse transmission and nervous excitation. Cancer- or tumor-promoting plant compounds are often used to induce cancerous conditions in experimental animals for purposes of screening and locating promising anticancer compounds, or for evaluating their potential effectiveness as pilot drugs. Agar, an extract from certain red algae, has remained unrivaled as a substrate for culturing medicinally useful microorganisms, while microbes *per se* are frequently employed in the transformation or fermentation of drug precursors into other, more desired drug compounds. For example, the antiviral compound Ara-A (adenine arabinoside) is now fermented by *Streptomyces antibioticus.* Thebaine, an alkaloid obtained from the great scarlet poppy (*Papaver bracteatum*) and the opium poppy (*P. somniferum*), is frequently converted by *Trametes saguinea* or other microbes to codeinone, a compound later converted to codeine or morphine. Likewise, many plant steroidal precursors are converted to steroids by *Mycobacterium* species.

Microbes also serve mankind as assay organisms for the analysis of drug products. In recent years, however, one of the most important assay organisms dis-

covered is the horseshoe crab, (*Limulus polyphemus*). Limulus is not a crab, but rather a distant relative of the spider. Horseshoe crabs may become an invaluable replacement for rabbits in biological assays for endotoxin, a fever-producing and sometimes fatal toxin produced by gram-negative bacteria. In order to prevent this toxin or the deadly bacteria from entering the bloodstream of patients, an appropriate assay organism is used to detect their presence in all pharmaceuticals and medical supplies or equipment destined to enter the bloodstream (e.g., intravenous solutions). The cost of *each* rabbit screening test has amounted to $10-75 in recent years; moreover, most of the test animals either die or are sacrificed after testing. In contrast, the "blood" cells (amoebocytes) of the horseshoe crab can be taken repeatedly from the same wild animals. Instead of injecting test compounds into an assay organism, the limulus amoebocytes are removed and their contents extracted. The extracts are then placed in a test tube with the test substance; if live or heat-killed bacteria are present, a congealing reaction occurs. The limulus assay is 10-15 times less costly than the rabbit assay; thus, it has been projected that a firm that conducts around 150,000 tests each year to satisfy FDA requirements might save $1 million annually. More important, the limulus assay is believed to be at least 5-10 times more sensitive than the rabbit test. Its accuracy may soon revolutionize the pharmaceutical industry. For example, a drug researcher using the limulus assay recently discovered six anticancer drugs that were contaminated with endotoxins even though they had been previously tested by rabbit assays and proclaimed free of them. He suggested that the toxic or other adverse effects associated with use of these and other chemotherapeutic drug compounds may actually be due to endotoxemia or bacterial contamination rather than to any toxic properties of the drug *per se*. If this turns out to be true, these pilot drugs may prove useful as chemotherapeutic agents once they have been purified and retested. Furthermore, modification of the limulus assay so that it can be used to test human blood samples might save as many as 250,000 lives annually. The threat of deadly infections by gram-negative bacteria is one of the greatest recovery problems that faces patients whose immune systems have been suppressed after organ transplants or other surgery. Hence, development of a diagnostic limulus test for these bacteria or for endotoxemia in human blood samples could save many lives by facilitating early treatment of septic or surgical shock.

The recent discovery of the limulus assay demonstrates the potential usefulness of wild animal species to medicine, especially since horseshoe crabs have not yet reproduced in captivity and therefore must still be harvested from wild populations. A great number of other wild animals have been obtained from natural environments to serve mankind as research subjects or models for drug development and testing and for biomedical research. The study of leprosy (*Mycobacterium leprae*), long a mysterious human disease, has recently been facilitated by experimental induction of the disease in the 9-banded armadillo (*Dasypus novemcinctus*). This species also regularly produces 4 genetically identical offspring from a single fertilized egg. It is hoped that study of reproduction in the armadillo may also help us to better understand "twinning" in humans and domestic animals, and thus aid us in dealing with some of the problems associated with monozygotic, multiple births. The fox squirrel (*Sciurus niger*) has provided a useful animal model for the study of a human genetic disease (erythropoietic porphyria). Treatment of cardiomyopathy, a disease caused by the overdevelopment of heart muscles, is being aided by studies of the extensive flight capabilities of albatrosses (*Diomedea* spp.) and the Storm Petrel

(*Hydrobates pelagicus*). A number of other species were obtained from the wild in relatively recent times for domestication and use as animal research models; these include the skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), and the currently endangered chinchilla (*Chinchilla laniger*) of South America. In addition, two species of frogs, the bullfrog (*Rana catesbeiana*) and the leopard frog (*R. pipiens*), have been harvested from the wild for decades to serve as invaluable laboratory specimens for students in the medical and health sciences. It was recently estimated that roughly 9 million frogs are used annually in the United States for research purposes. One subspecies of leopard frog found near Las Vegas, Nevada (*R. pipiens fisheri*) is currently endangered due to habitat loss and introduced bullfrogs.

In spite of the important contributions of these wild animals, no group of biomedical research animals is more important to mankind than the nonhuman primates. Although some of the primates used for research purposes are obtained from captive breeding populations, many species cannot be successfully reared in captivity. During the late 1950's and the 1960's, hundreds of thousands of primates were imported annually into the United States for biomedical or other research purposes. In 1972-1973 from two-thirds to three-fourths of the primates imported into our country were used for biomedical research and drug testing purposes. Nearly all of these animals were exported from tropical countries. The principal biomedical research value of non-human primates derives from their physiological, biochemical, morphological, and embryological (developmental) similarities to humans. For example, the drug-induced and disease-induced reactions of nonhuman primates very closely mirror those observed in humans. Consider the thalidomide tragedy of the late 1950's and early 1960's. This antiemetic and tranquilizing synthetic drug caused severe birth defects in children born to an estimated 10,000 women in Germany and other parts of Europe. The most common congenital malformation observed was phycomelia, a shortening or lack of limbs; other anomalies included paralysis of the cranial nerves and absence of external ears. In the years following this tragedy, virtually the same birth defects were experimentally induced in fetuses of macaque monkeys (*Macaca irus* and *M. mulatta*) and yellow baboons (*Papio cynocephalus*). Discovery of basically identical dose-effect relationships in both pregnant humans and pregnant nonhuman primates ushered in a new era of drug safety testing and fetal pharmacology. It also let to the suggestion that an appropriate primate model should be used for testing all drugs destined for use in pregnant women. However, this has not yet become a mandatory requirement, in great part due to the lack of a stable, foreign or domestic source of nonhuman primates, and the great expense associated with the testing process.

Other striking similarities between humans and other primates can also be cited. These highlight the great value of nonhuman primates as research models, experimental subjects, and even as organ donors. For example, baboon livers have been used temporarily in humans to aid their recovery from liver failure of hepatic coma. Baboons (*Papio* spp.) have also been particularly valuable for dental research and experimental surgery, while the chimpanzee (*Pan troglodytes*) has been extensively used in behavioral and animal communication studies as well as in psychobiology. The study of cardiovascular diseases has been aided by the squirrel monkey (*Saimiri sciureus*), and the African vervet monkey (*Cercopithecus aethiops*) has played an essential role in toxicology and pharmacology studies. Some species have been unique

contributors to major advances made in the study of certain infectious diseases. For example, during the 1960's, antimalarial synthetics were crucially needed to help U.S. troops in Southeast Asia when commonly used synthetics were discovered to be ineffective against a drug-resistant strain of malaria (*Plasmodium falciparum*). Research efforts were hampered by the lack of an appropriate animal research model—a primate species that could be successfully infected with both drug-resistant and drug-susceptible strains of this human blood parasite. Finally, a previously unknown experimental research species, the owl monkey (*Aotus trivirgatus*) of South America, was demonstrated to exhibit virtually the same responses to the malarial strains as those observed in U.S. troops. As a result of this discovery, a procurement program was initiated from the lowland tropical rain forests of Colombia, and thousands of owl monkeys were imported annually to the United States for many years. Certain primate species have also served as valuable animal models for the study of other human diseases: leaf monkeys (*Presbytis* spp.) for bubonic plague, Celebes macaques (*Macaca maura*) for diabetes, marmosets (*Callithrix* and *Saguinus* spp.) for hepatitis and cancer, and woolly monkeys (*Lagothrix* spp.) for leukemia.

Primates are also essential for the study of reproductive physiology, arteriosclerosis and other chronic degenerative diseases, mental health, malnutrition, and drug metabolism and drug abuse; further, they are also valued for production of human vaccines. Table 2 lists the most important nonhuman primate species used for drug development and evaluation, vaccine production, and biomedical research; the principal source of these invaluable resource species has historically been tropical forests. However in recent years, use of primates for research purposes in the United States and most other industrialized economies has declined significantly due to inflationary costs coupled with lack of availability of primates from tropical countries that have recently imposed export bans.

Considering the great importance of medicinally useful biota as indirect contributors to the productivity of the medicinal and health services sector of the U.S. economy, it is mandatory that we take a greater interest in the conservation of their wild breeding populations and the natural environments that sustain them. For the most part, medicinal gene resources are obtained from tropical forests and warm seas, so these areas should be a principal focus of such conservation efforts. Without *in situ* as well as *ex situ* conservation, many of these species will become extinct or severely reduced in number as a result of overexploitation and habitat destruction within the next few decades.

Recent Discoveries of New Anticancer Drug Compounds

Cancer comprises a variety of neoplastic diseases (Greek: *neos*-new, *plasma*-formation) characterized by changes in cells that lead to their unordered and uncontrolled proliferation in the body. It is commonly found in all animal species, except many lower life forms; and even plant species can develop cancerlike growths. Cancer is known to affect all human populations, and its incidence has increased greatly in recent times. During past decades, the annual incidence of cancer in the United States was less than about 1.1 percent; however, by 1975 the rate had risen to 5.2 percent. In that same year, the director of the National Cancer Institute, Frank J. Rauscher, Jr., estimated that by 1985, nearly 4 million Americans would die from cancer, and more than 10 million would be treated for cancerous diseases. This

TABLE 2. Principal Primate Species Imported by the United States for Biomedical Research During the 1970's

Species	Native Distribution & Habitat	Principal Use of Species (Conservation Status)
Aotus trivigatus (Owl/night monkey)	Central & South America—savanna & all forest types	Infectious disease (malaria chemotherapy); sensory; cancer research (viral oncology); vision research. (Some countries prohibit export.)
Callithrix jacchus (Common marmoset)	Eastern Brazil—tropical forests	Reproductive physiology (antifertility product testing); teratology; toxicology; drug safety testing; infectious disease; behavior. (Protected throughout range.)
Cebus spp. (Capuchin monkeys)	South America—tropical forests	Cancer research; pharmacology & toxicology; physiology. (Available for trade.)
Cercopithecus aethiops (African vervet monkey)	Subsaharan Africa—woodlands, savannas & rainforests	Pharmacology & toxicology; kidney tissues for SV40 virus-free poliomyelitis vaccine; hypertension studies; cancer research; infectious disease. (Available for trade.)
Hylobates spp. (Gibbons)	S.E. Asia & Indonesia—primary tropical forests	Cancer virus & hepatitis B research; behavioral studies. (Endangered & protected.)
Macaca arctoides (Stumptail macaque)	Burma to Indochina & China—forests	Neurophysiology; organ system diseases; sensory studies; experimental surgery. (Protected throughout range.)
Macaca fascicularis (Long-tail macaque)	Burma to E. Indies & Philippines—secondary forests	Pharmacology & toxicology; behavior; reproductive physiology; organ system diseases. (Available for trade.)
Macaca mulatta (Rhesus macaque)	India & neighboring countries—forests and woodlands	Poliomyelitis & other vaccine safety testing; pharmacology & toxicology; neurophysiology; infectious disease; sensory; reproductive physiology; behavior; psychobiology; diseases; organ systems. (Some populations declining; Most countries prohibit export.)
Macaca nemestrina (Pig-tail macaque)	Assam to Indo-Malaysia—hill and lowland forests	Research purposes: sensory, behavioral, and physiological (reproductive). (Available for trade.)
Pan troglodytes (Chimpanzee)	West Africa; also Tanzania & Uganda—forests	Psychobiology; infectious disease (especially hepatitis); drug safety testing & vaccine production. (Endangered and protected.)
Papio spp. (Baboons)	Subsaharan Africa—forests, savannas & altered habitats	Experimental surgery; reproductive physiology; neurophysiology; physiology; general purposes. (Available for trade.)
Saguinus spp. (Tamarins)	South America—tropical and montane forests	*S. mystax*—hepatitis A virus research; *S. oedipus* (endangered)—viral oncology; other spp.—immunology, virology, reproductive physiology; behavior; dental research. (Some countries prohibit export.)
Saimiri sciureus (Squirrel monkey)	Central & northern South America—forests	Pharmacology & toxicology; neurophysiology; cancer research; behavior; organ system diseases; drug safety testing & vaccine production. (Available for trade.)

Sources: Schmidt, 1972; NAS, 1975; Interagency Primate Steering Committee, 1978; Mack, personal communication.

means that within that decade, nearly two of every three American families will have some experience with cancer, with total medical care costs amounting to around $15-20 billion each year. Clearly, unless better preventative and curative methods for cancer are discovered or devised, approximately 53 million Americans alive now will ultimately be cancer patients.

The best hope for the future lies in prevention and treatment. Prevention includes control over radioactive and carcinogenic compounds, dietary factors (e.g., tobacco, alcohol, and causative agents in foods and drugs), and cancer-inducing viruses; while improved treatment focuses on the discovery and development of new anticancer drugs and other means to effect cures. Ample evidence indicates that even if major surgery removes most of a cancerous growth, microscopic foci of tumor cells may be left behind. Some of these will eventually grow into a new tumor that often leads to the patient's death. These tumor cell foci are usually combated with radiotherapy and chemotherapy after surgery. In addition, the latter therapies may be used in lieu of surgery.

One important facet of past and current efforts to locate new cancer drugs is the search for natural sources of compounds with anticancer activity. As in the case of most major therapeutic drug categories, many are obtained synthetically; however, plants, animals, and microbes still serve as important, original sources of novel anticancer compounds for drug development. Table 3 lists naturally derived drugs introduced into cancer chemotherapeutic practice since the origin of the National Cancer Institute's (NCI) Developmental Therapeutics Program (DTP) in 1956. Interest in natural sources of anticancer drugs actually began with the success of the catharanthus (vinca) alkaloid drugs—vincristine sulfate and vinblastine sulfate. These are often referred to as the first modern cancer drugs, and vincristine has been hailed as a miracle drug for playing a major role in curing or effecting extensive remissions of acute childhood leukemias. A remission rate of 99 percent, with 50 percent survival after 3 years, has been produced by vincristine in combination with prednisone—a synthetic drug modeled after the naturally derived steroid, cortisone—and daunorubicin—a microbial drug that has been replaced by the related drug, doxorubicin from *Streptomyces peucetius* var. *caesius.*

The medicinal value of the red periwinkle (*Catharanthus roseus*) of Madagascar (Fig. 6), a tropical perennial herb, was not recognized scientifically until the early 1950's. At that time, Canadian researchers were investigating folkloric reports of a catharanthus leaf tea used in the West Indies as a treatment for diabetes. Since then, the two catharanthus drugs have proved effective against an array of cancerous conditions: testicular, cervical, and breast cancers; Hodgkin's disease and other malignant lymphomas; solid tumors, Wilms' tumor, and primary brain tumors; choriocarcinoma; and malignant melanoma. For example, vincristine used with dactinomycin, surgery, and radiotherapy has produced an 80 percent cure rate for Wilms' tumor, while vinblastine used with dactinomycin, mithramycin, and a synthetic drug, methotrexate, has resulted in a 70-95 percent cure rate for choriocarcinoma. Dactinomycin, doxorubicin, and the other microbially derived anticancer drugs currently in use are derived from *Streptomyces* bacteria. In addition, the two drugs originally derived from animal sources noted in Table 3 are now produced either synthetically or by microbial fermentation.

The effort to locate natural sources of anticancer drugs was an important part of the NCI's comprehensive drug development program. In the two decades between

TABLE 3. Natural Sources of Anticancer Drugs in Use in the United States (1980)

Original Biotic Source(s)	Drug(s)	Uses and Other Notes
Plants:		
Catharanthus roseus (Red or Madagascar Periwinkle)	Vinblastine sulfate (Velban®)	Hodgkin's disease (one of the most effective treatments known); testicular & breast carcinomas; choriocarcinoma; lymphocytic & other lymphomas.
	Vincristine sulfate (Oncovin®)	Acute leukemias; Hodgkin's disease; Wilms' tumor; reticulum-cell and other sarcomas; neuroblastoma.
Animals:		
Cavia porcellus (serum) (Guinea pig; also other members of Caviidae)	L-asparaginase (Elspar®)	Acute lymphocytic leukemia (30-60%); used with other drugs; it is now obtained from *Escherichia coli B, Serratia marcescens,* and plant pathogens of the genus *Erwinia.*
Cryptotethya crypta	Cytarabine; Cytosine arabinoside (Ara-C; Cytosar-U®)	Acute myelocytic leukemia and other acute leukemias; cytosine arabinoside is a synthetic compound modeled after the β-D-arabinosyl nucleosides obtained from this marine animal.
Microorganisms:		
Streptomyces caespitosus	Mitomycin-C (Mutamycin®)	Adenocarcinoma of stomach or pancreas (in combination with other drugs).
Streptomyces parvullus and *S. chrysomallus*	Dactinomycin (Actinomycin D; Cosmegen®)	Wilms' tumor & gestational choriocarcinoma (70-90% cure rate); testicular carcinoma; soft tissue and other sarcomas.
Streptomyces peucetius var. *caesius*	Doxorubicin hydrochloride (Adriamycin®)	Bladder, thyroid, breast, & ovarian carcinomas; soft tissue & bone sarcomas; certain leukemias; Wilms' tumor; solid tumors; Hodgkin's & non-Hodgkin's type lymphomas.
Streptomyces tanashiensis	Mithramycin (Aureolic acid; Mithracin®)	Testicular malignancies (esp. of embryonal type); hypercalcemia & hypercalciuria associated with many neoplastic diseases; now obtained from *S. plicatus.*
Streptomyces verticillus	Bleomycin sulfate (Blenoxane®)	Hodgkin's disease & other lymphomas (30-60%); testicular carcinomas (40-70%); squamous cell carcinomas (20-40%).

Sources: Lewis and Lewis (1977); Pettit (1977); *Physicians' Desk Reference,* vol. 34 (1980).

Fig. 6. The red or Madagascar periwinkle *(Catharanthus roseus)* was initially investigated as a possible treatment for diabetes. However, researchers discovered its anticancer activity, and further investigation yielded the first modern anticancer drugs. (Illustration: Agricultural Research Service, USDA)

1956 and 1976, 200,000 plant extracts, 150,000 microbial cultures, and 27,000 animal extracts (primarily marine in origin) were tested for cell cytotoxicity or for anticancer activity in experimental animal systems. By 1977, 3,585 potentially useful extracts derived from 2,591 plant species had successfully demonstrated reproducible results in preliminary screen tests. Thus the anticancer activity of the plant extracts screened was roughly 2 percent, while the percentage of active species located was between 8 and 10 percent. Although the yield of potentially useful anticancer extracts may seem low, it should be remembered that when the value and effectiveness of penicillin for treating bacterial infections was first recognized, it prompted a massive screening program for other natural antibiotic substances; however, the ensuing search of about 10,000 mold and bacteria species yielded only 10 percent with effective antibiotic activity. Only half of these were nontoxic enough to warrant further investigation for human use. Despite these difficulties, by the early 1970's almost 1,000 antibiotics had been patented or described in the literature. And from these, we have obtained most of the antibiotics in common use today.

The plant screening and research program sponsored by NCI and conducted by the USDA Economic Botany Laboratory in Beltsville, Maryland resulted in a number of promising discoveries. An important focus of the USDA's plant procurement program included use of folkloric literature and folk knowledge to reveal potential anticancer compounds as well as knowledge of botanical relationships (families or genera of plants that have demonstrated biological activity). Although some problems are associated with reliance on folk knowledge, this method can yield significantly more active species than other approaches. Two researchers associated with this program during the 1960's concluded that the yield of active species would probably have been increased by 50 percent, possibly by 100 percent, if the anticancer screening process had been guided solely by folk knowledge of medicinal and poisonous plants.

The most promising plant and microbial anticancer compounds currently in various stages of drug development in the NCI program are listed in Table 4. Those which have been dropped due to toxicity or other problems, or which have shown little promise after phase II of clinical testing (the first phase of extensive human testing) are not included. Two compounds located via the use or study of native U.S. plants are taxol and 4′-demethylepipodophyllotoxin. Taxol is a diterpene compound derived from the western yew of the Pacific Northwest, *Taxus brevifolia.* The other compound was obtained from the Indian mandrake (*Podophyllum emodi*), following the extensive work completed earlier in the United States on a related compound, podophyllotoxin (see Table 1), derived from the related American species, *P. peltatum*. The underground stems (rhizomes) of the American mandrake were once used by the Penobscot Indians of Maine to treat cancers, and the Cherokee Indians have used the rhizome extracts to relieve deafness. It was also valued as an emetic and purgative. When European settlers arrived on the American continent, they adopted the use of this medicinal herb. Crude mandrake extracts became officially used in the United States during the 19th century; by 1864 podophyllin extract was employed for cancerous tumors, granulations, and polyps, though it was also used as a laxative and purgative. Since 1897 podophyllin resin has been an effective treatment for venereal warts. As a result of the widespread use of this toxic plant, it has been harvested from the wild and even cultivated (Fig. 7) in the northeastern United States for quite some time. In 1947, the potential usefulness of podophyllotoxin as

Fig. 7. The American mandrake *(Podophyllum peltatum)* (left) and blood root *(Sanguinaria canadensis)* (right-center), plants traditionally used in American folk medicine for treating cancerous conditions, are shown growing together in cultivated stands. (Photo: Agricultural Research Service, USDA)

an anticancer compound was demonstrated in animal tests; however, it was later dropped during early clinical trials due to toxicity and other problems. Interest in the compound, however, led to the discovery of other plant podophyllotoxins, including epipodophyllotoxin derived from the Indian mandrake, *P. emodi.* Chemical modifications of this natural molecule produced the semisynthetic pharmaceutical compounds, VM-26 and VP-16-213. Some early trials with these showed that VM-26 might be beneficial for treating brain tumors, Hodgkin's disease, and non-Hodgkin's lymphomas, and that patients with acute granulocytic leukemia might respond favorably to VP-16-213 therapy. Currently, both drug compounds are undergoing more extensive clinical trials to determine whether they can be used directly or modified for use as new anticancer drugs. One of them has already shown promise for treating a type of lung cancer.

Although some native American species and a few nonnative species were obtained from domestic sources for NCI's plant screening program, most of the plant materials obtained for testing and evaluation were procured from foreign environments, especially many tropical countries (Figs. 8-9). One anticancer compound which shows promise for treating certain leukemias is indicine N-oxide from the toxic, pantropical weed of the Boraginaceae family, *Heliotropium indicum* (Fig. 10). This promising compound has passed preclinical and phase I clinical trials, and is now in phase II of clinical testing. The results so far have been encouraging, and indicine N-oxide will probably become one of our next anticancer drugs. Oddly this substance belongs to a family of chemical compounds known to induce liver cancer—the pyrrolizidine alkaloids.

Fig. 8. Laborers harvesting a giant lily plant from an Ethiopian forest. Plant species collected by the USDA Economic Botany Laboratory for the National Cancer Institute's plant screening program were located during the 1970's in a worldwide search for new sources of anticancer compounds. (Photo: Agricultural Research Service, USDA)

Fig. 9. Plant material drying beds in Jilore, Kenya in 1969. A tarpaulin is being removed from drying beds that contain materials from various species of tropical plants. Most of the species initially procured for screening and evalaution for anticancer activity in the USDA-NCI research effort were obtained from tropical environments. (Photo: Agricultural Research Service, USDA)

Fig. 10. The very promising anticancer compound, indicine N-oxide, is found in the leaves, stems, and fruits of *Heliotropium indicum*. (Illustration: Agricultural Research Service, USDA)

Another promising anticancer compound being evaluated in this plant screening program is bruceantin, from *Brucea antidysenterica* (family Simaroubaceae). Bruceantin belongs to a group of terpene-related compounds, the quassinoids, which are well known in folk medicinal history. In fact, *Brucea antidysenterica* (Fig. 11), a common Ethiopian tree, has a long history of folk use for treating both dysentery and cancer. Bruceantin, also in phase II of clinical evaluation, is concentrated primarily in the stem bark. However, a rare species, *B. guineensis,* contains the active compound throughout the entire plant. The latter species may therefore be used as a superior source of bruceantin if it becomes a useful drug that cannot be obtained more cheaply by synthetic means.

In addition to the promising anticancer substances that have been isolated from plant and microbial sources, about 27,325 marine animal extracts were screened between 1972 and 1977. Of these, 617 (from 525 species) (about 2 percent) showed significant activity in at least one standard screening test. One group of researchers screened 1,600 extracts, with 9 percent of those showing significant activity on initial evaluations. In addition to their anticancer activity, many of these extracts have shown some potential for treatment of cardiovascular and central nervous system afflictions. The most notable compounds isolated thus far from a marine animal are the β-D-arabinosyl nucleosides, spongothymidine and spongouridine, isolated in the 1950's from *Cryptotethya crypta,* a Caribbean sea sponge. Isolation and purification of these compounds led eventually to the synthesis of cytosine arabinoside (Ara-C), a compound related to adenine arabinoside (Ara-A), mentioned previously for its antiviral properties. Today Ara-C or cytarabine is synthesized chemically for treating certain leukemias. Other compounds obtained from marine animals which show anticancer activity include those from coelenterates: palytoxin from *Palythoa toxica* (a zoanthid) of Hawaii and stoichacetin from *Stoichactis kenti* (a sea anemone) of Tahiti; compounds from nudibranchs (sea hares), including aplysistatin from *Aplysia angasi* and dolatriol 6-acetate from *Dolabella auricularia* of the Indian and Australian Oceans; and substances from echinoderms, for example, actinostatin I and stichostatin I from the sea cucumbers, *Actinopygia mauritiana* of Hawaii and *Stichopus chloronotus* of Australia. It is interesting to note that a sea cucumber related to *Stichopus chloronotus, S. japonicus,* is frequently marketed in Asia for various medical treatments.

In addition to marine animals, about 4 percent of the extracts evaluated in the early 1970's from 800 species of terrestrial arthropods (insects, spiders, crustaceans, millipedes, and centipedes) showed some anticancer activity. The more promising compounds included isoguanine and isoxanthopterin from the Asian butterflies *Prioneris thestylis* and *Catopsilia crocale,* respectively, and dichostatin from the Taiwanese stag bettle, *Allomyrina dichotomus.* The active constituents were concentrated in the wings of the Asian butterfly (*C. crocale*) and in the legs of female stag beetles. It is of interest that early studies of butterfly wing compounds enabled some of the advances in anticancer chemistry which facilitated the synthesis of methotrexate, a synthetic cancer chemotherapeutic drug currently in clinical use in the United States. Very few of the higher land animals have yet to be even superficially examined for active anticancer compounds. However, some poisons and venoms, noted for their cardiac and analgesic effects, have been chemically isolated and screened, for example, marinobufagin, a poison, from the giant marine toad, *Bufo marinus,* and cobra and viper snake venoms.

Fig. 11. *Brucea antidysenterica,* a small tree, the source of the anticancer compound bruceantin, is widely distributed throughout the tropical African highlands, but apparently it is abundant only in Ethiopia. (Illustration: Agricultural Research Service, USDA)

TABLE 4. Natural Sources of Anticancer Compounds Undergoing Drug Development in the U.S. National Cancer Institute Developmental Therapeutics Program (1980)

Original Biotic Source	Geographic Source	Drug Compound	Compound Type
Plants:			
Baccharis megapotamica (or *Fusarium* sp. symbiont)	Brazil	Baccharin	Trichothecane
Brucea antidysenterica	Ethiopia	Bruceantin	Quassinoid
Cephalotaxus harringtonia var. *drupacea*	China, Japan	Homoharringtonine	Alkaloid
Excavatia coccinea and *Ochrosia moorei*	New Guinea, Australia	Ellipticine	Alkaloid
Heliotropium indicum	India	Indicine N-oxide	Alkaloid
Podophyllum emodi	India	4'-Demethylepi-podophyllotoxins (VM 26; VP 16-213)	Lignan (semisynthetic)
Taxus brevifolia	United States	Taxol	Diterpene
Microorganisms:			
Streptomyces nogalater; also *S. galilaeus*	Japan	Aclacinomycin A Nogamycin	Anthracycline antibiotics
Streptomyces parvullus; also *S. antibioticus*	United States	Actinomycin Pip 1β	Peptide antibiotic
Streptomyces svicus	United States	Antibiotic AT-125	Isoxazole

Sources: Pettit 1977; Douros and Suffness 1978; Suffness and Douros 1979; Suffness, personal communication.

On October 2, 1981, the USDA plant and animal screening programs were eliminated from the DTP program during the NCI budget-paring process, while the emphasis on investigation of synthetic analogs of active drug compounds and microbial fermentation processes was basically retained. Within the near future, the DTP program will focus its efforts on natural compounds that have already been isolated from plant or animal sources and purified chemically, thus eliminating the costly process of procuring large quantities of biological materials and chemically extracting compounds from them. Therefore, rather than relying on knowledge of folk medicine or biological activity to discover novel drug sources, or on random screening of uninvestigated species, the NCI program will now focus instead on screening and evaluation of chemical compounds that have already been located, isolated, and purified for some reason—not necessarily drug-related.

Meanwhile, the plant and animal screening projects are being reevaluated; and in time, their relative shortcomings and successes will be ascertained. Nevertheless, we do know that folkloric medicine has validity as a source of useful pharmaceuti-

cals; the record, as exemplified by Table 1, demonstrates this. We also know that natural compounds which show biological activity against particular diseases are often good lead compounds for the discovery of analogs (related compounds) that also show promising pharmacologic activity or are effective for treating very different diseases. Natural products *do* have value as cancer chemotherapeutic agents, as evidenced by Tables 3 and 4; however, we are not certain at present how to best go about locating promising natural sources of anticancer compounds, or the best way to assay them. Only time will tell whether the new NCI approach will be generally more successful and cost-effective than the former one. Yet, by the time we decide which option seems best, many of the human cultures and specific people that know about obscure medicinal biota will have disappeared, as well as many of the potentially useful medicinal species which they highly value.

Genetic Improvement of Medicinal Biota

Genetic improvement of medicinally useful microorganisms, particularly by artificial induction of mutations, is a relatively common practice. For example, after the discovery of the high-yielding penicillin-producing species *Penicillium chrysogenum* (Fig. 2), even more productive strains were obtained by X-ray and ultraviolet radiation. However, genetic improvement of medicinal crop plants has been only rarely attempted, even though striking genetic differences among individuals or among geographic or "chemical" races of many medicinal plants have been documented. It is not uncommon to find one chemical race or species that possesses good quantities of a desired pharmaceutical compound while others are completely devoid of it. A vast literature on genetic improvement of plants from the agricultural sciences indicates that applied plant breeding programs could lead to significant enhancement of the quality and quantity of active drug constituents in species cultivated for medicinal purposes. For example, alkaloids and other medicinally important compounds are under varying degrees of genetic control in plants. A University of Illinois drug improvement program in the 1940's produced genetically improved, high-yielding varieties of belladonna (*Atropa*), jimson weed (*Datura*), and henbane (*Hyoscyamus*) through applied breeding and selection. This program was also successful in producing improved, higher-yielding strains of foxglove (*Digitalis*). Moreover, in India where many drug plants are commonly cultivated for domestic use as well as commercial export, progress is being made in selecting better, higher yielding strains of ergot (*Claviceps purpurea*), opium poppy (*Papaver somniferum*), and dioscorea (*D. floribunda* and other species). In addition, different geographic races of Indian serpent-wood (*Rauvolfia serpentina*) differ in their average content of the active rauwolfia alkaloids, and currently much attention is being paid to the selection of high-yielding strains of this tropical evergreen shrub as well. It is of interest that Hawaii harbors three species and three distinct subspecies of rauwolfias that may now be threatened with extinction. Do any of these disappearing taxa contain genetic materials that could be useful to Indian drug plant breeders?

History of the Improvement and Use of Quinine

The exploitation of wild germplasm to enhance the productivity of a medicinal

plant species is perhaps best exemplified by the history of the genetic improvement and use of quinine (*Cinchona ledgeriana* and *C. calisaya*). The bark of tropical American cinchona trees contains quinine and other medicinally useful alkaloids, e.g., cinchonine, cinchonidine, and quinidine. The last effectively treats heart fibrillations, while the primary role of quinine is to treat malaria, a parasitic infection of the blood caused by *Plasmodium* spp. transmitted to humans only by *Anopheles* mosquitoes. Prior to the European discovery of the New World, Andean Indians had apparently employed cinchona bark extracts to combat malaria since early times; however, European recognition of its value required a half century after it was first introduced to that continent.

The European discovery of cinchona's efficacy against malaria led to commercial extraction of "Peruvian bark" from the tropical montane forests in the Andes of South America. Large amounts of the bark were exported to Europe during the 17th and 18th centuries, and until 1850, all quinine came from this area. By 1880, South America was still the major exporting region, producing 3.2 million kg (7 million lb) of wild quinine bark, or 85 percent of the total world trade, in that year; Colombia was the world's leading exporter, producing more than 2.7 million kg (6 million lb). But by the mid-1800's, the heavy demand for quinine had already resulted in the severe depletion of many of the wild South American stands, and production gradually began to decline.

By 1850, the increasing scarcity of wild cinchona trees became a source of concern to importers in the United Kingdom and the Netherlands. Exhaustion of natural supplies of quinine would have greatly affected their ability to operate and hold certain tropical colonies. Thus, in the late 1850's both nations dispatched expeditions to South America to gather germplasm, so that plantations could be established in their Asiatic colonies. A number of cinchona seeds from Bolivian trees were harvested by a British explorer named Charles Ledger with the help of his servant Manuel. Ledger unknowingly obtained seed of a relatively high-yielding gene resource species (7 percent dry weight quinine); he later peddled the seeds to the Dutch government. Through breeding and careful selection among the progeny of Ledger's wild tree stocks, strains yielding up to 17 percent of the valuable antimalarial alkaloids were eventually developed; the cultivated species (*Cinchona ledgeriana*) now bears his name.

The high-yielding strain *C. ledgeriana* (presumably derived from *C. calisaya*) grafted onto more vigorous, disease-resistant *C. succirubra* rootstocks, served as the biotic basis for the successful Far Eastern quinine plantations. Thus, more than three centuries after quinine bark was initially discovered in the Americas by Europeans, the first wild cinchona trees were introduced to Java by the Netherlands government. Within 60 years, nearly 80-90 percent of the world production of quinine became centered in Java, and the Dutch controlled a virtual monopoly. British entrepreneurs in Ceylon and British India were unable to hold their earlier lead (1880's) in the world market, primarily because they had obtained wild *C. succirubra* and *C. officinalis* which contain typically only 0.1-3.0 percent quinine by dry weight. Thus, these species yielded comparatively low amounts of the desirable antimalarial alkaloids. Yet, all of the early 20th century commercial plantations easily outcompeted the Latin American harvesters, for the Asian producers relied on cultivated stands of genetically improved wild trees. In contrast, the New World producers depended on the exploitation of scattered populations of unselected wild cin-

chona trees, and many of these had been severely depleted during the early years of quinine production. Thus, both overexploitation and competition from Asian producers who relied on improved, cultivated cinchona populations contributed to the ultimate downfall of the wild resource-based monopoly in the Americas. By 1933, 10 million of the 11.7 million kg (22 million of 25.8 million lb) of cinchona bark produced worldwide originated in the Dutch East Indies.

World War II left the Allied Forces with hardly any quinine after Japan occupied Java (Indonesia) and Sumatra in March 1942. Overnight, 85-90 percent of all commercially produced cinchona bark was suddenly inaccessible to quinine users of the Western Hemisphere. Meanwhile, the Allied Forces were forced to undertake military operations in malaria-infested tropical areas, while the Japanese and Germans were relatively protected. They not only controlled the Asian quinine-producing region, but they also had synthetics. In 1932 the Germans had successfully perfected the synthesis of the antimalarial drug atabrine using coal-tar sources (this situation can be likened to the simultaneous rubber crisis discussed in Chapter 6). The political and economic welfare of the United States was, in part, tied to the abandoned natural stands of wild cinchona in Peru, Colombia, and Ecuador, and some pre-war plantings in Costa Rica. During the war, the United States successfully procured 5.7 million kg (12.5 million lb) of dried bark from South America in 1943-1944. Additionally, new plantations were hurriedly initiated in Guatemala with seedlings of *C. succirubra,* and in Costa Rica, with seedlings of the high-yielding *C. ledgeriana,* which Col. Arthur Fischer had heroically rescued from a plantation in Mindanao. Other plantations were initiated in East Africa, the Congo, Mexico, and Peru. However, since it takes approximately 10 years to produce adequate quantities of cinchona bark from young plants, these new plantings did not contribute to the war effort. Following the war, many positive steps were taken to avoid another such crisis, the most important being the establishment of a USDA collection of superior *Cinchona* germplasm in Guatemala in the late 1940's. Unfortunately, this valuable collection was not maintained, in part because synthetic antimalarials, first synthesized in the United States in 1944, began to slowly replace the need for natural quinine.

During the Vietnam conflict, *Plasmodium* strains resistant to synthetic quinines began to proliferate in Southeast Asia. A crisis ensued, and natural quinine again assumed importance, for despite the fact that troops were taking a preventative synthetic derivative weekly, combat forces were experiencing a malarial attack rate of roughly 1 percent per combat day. A 1973 World Health Organization report described the situation as follows:

> The use of quinine, the oldest of all the antimalarial drugs, had declined with the introduction of the 4-amino-quinolines. However, with the emergence of resistant strains of *P. falciparum* to these and other synthetic antimalarials, quinine is again being widely used in the management of acute falciparum infections (p. 15).

Intense efforts were made to prepare new antimalarial and antibiotic treatments for nonimmune (nearly all Caucasian) U.S. troops in Southeast Asia. However, this time the development of adequate malaria chemotherapy was hampered by the lack of an animal model that was susceptible to strains of the human *Plasmodium* parasite. The problem persisted until 1966 when the owl monkey (*Aotus trivirgatus*) was found to be suitable. Quinine derived from both wild and cultivated plants was used successfully in combination with antibiotics and synthetic derivatives until new chemotherapeutic regimens could be developed for treating ailing U.S. soldiers.

U.S. vulnerability with respect to *Cinchona* availability during two different wars highlights the importance of *ex situ* and *in situ* conservation of such medicinal gene resources. In spite of our experience we have given very little attention to the conservation and use of *Cinchona* genetic diversity within the Western Hemisphere. Thus, lack of foresight may plague the United States again in the event of a new national emergency. The few commercial tropical plantations scattered around the globe are testimony to the recent demand for quinidine and the partially renewed demand for quinine to combat the increasing number of *Plasmodium* strains resistant to commonly used synthetics. However, the genetic base of most of these planted stocks is very narrow. Although much progress has already been made with respect to improvement of alkaloid yields and some other desirable agronomic traits (e.g., thicker bark, improved bole shape) within stocks of *Chinchona ledgeriana,* most of the breeding potential of the wild species remains unexploited and largely uninvestigated. In recent years, Asian cinchona producers have suffered from the effects of overproduction. Thus, on the part of some people involved in the industry itself, the urgency of the short-term situation strongly overshadows any perceived need for the further use and conservation of *Cinchona* germplasm. Nevertheless, the adequacy of the germplasm base in Guatemala and other cinchona-producing regions of the Western Hemisphere should be re-evaluated, especially since a more comprehensive collection of gene pool resources could facilitate present breeding efforts as well as preserve germplasm for future needs or crises. In addition, more attention should be paid to conservation of overexploited populations of owl monkeys in the lowland coastal rain forests of Colombia, as well as other depleted or endangered populations of nonhuman primates.

Major Losses of Medicinal Gene Resources

Heavy demand for biomedical products from natural sources—for either folk or modern medicine—can result in the extinction or depletion of valuable wild breeding populations. The species most vulnerable to extinction are those that are naturally rare and must be sacrificed to yield the desired product(s), yet are long-lived, slow-maturing, and difficult to cultivate or domesticate. In addition, habitat destruction, especially the rapidly accelerating deforestation of the tropics, takes a heavy toll on medicinally useful biota (particularly populations of nonhuman primates). In fact, tropical deforestation currently extinguishes an estimated one to two taxonomically unknown species each year. Since tropical regions serve as our most important sources of potentially useful medicinal products and novel pharmaceutical compounds, the irretrievable loss of many of these unknown species is likely to correspond to the loss of potential drugs or biomedical research species.

Finally, the incursion of modern civilizations and large-scale development projects into the few sizeable tracts of natural environments that remain on earth continues to alter or destroy the cultures of the remaining indigenous societies. As these societies are lost or become "modernized," the traditional customs and indigenous folk knowledge regarding medicinal uses of plants and animals disappear with them. Indigenous peoples' knowledge of medicinal biota should not be underestimated. Most of the major medicinal plants still in use today have a long history of folk use, and their modern-day uses were, for the most part, discovered from study of traditional medicinal practices or societies. More than 200 drugs listed in the U.S.

pharmacopoeia prior to the development of synthetic drugs were obtained from study of American Indian cultures. One notable example is podophyllin (from American mandrake or May apple). One can only speculate as to how many other invaluable drug products could have been added to the list of those currently in use had such cultures not been progressively destroyed first. For example, one of the last members of the dying native Hawaiian culture—an elderly woman who had experienced traditional Hawaiian medical practices on Molokai—suggested that tentacles of the tropical seaworm, *Lanice conchilega* or "kaunaoa," be tested for anticancer activity. The crude tentacle extracts were found to inhibit tumor growth in 60-100 percent of the mice treated with it.

The Attrition of Medicinal Gene Resources

A number of higher plant species, including dioscorea (*Dioscorea* spp.), serpent-wood (*Rauvolfia* spp.), American ginseng (*Panax quinquifolium*), and quinine (*Cinchona* spp.), have been directly overexploited for the commercial drug trade—either folk or modern. All are relatively long-lived perennials, and for each, the primary harvesting strategy has required the sacrifice of individuals or entire populations, i.e., dioscorea for its underground tubers, ginseng and serpent-wood for their roots, and quinine for its bark. Although all of these species can be cultivated, it has often been cheaper or easier to harvest plants from accessible wild populations. Consequently, many resource populations became so scarce that either cultivation or location and development of alternative sources of the desired drug compound became the more cost-effective endeavor. By that time, important populations of these medicinally valuable species had already been depleted. Clearly, such practices are neither in the interest of the survival of the medicinally important species, nor of ultimate cultivation or domestication efforts. In the latter case, the loss of distinct populations means loss of valuable germplasm resources that could have otherwise been available for genetic improvement of drug plants, e.g., for disease resistance or increased yield. Populations comprised of high-yielding individuals may have been especially vulnerable to extermination due to their greater value as sources of drugs.

The cinchona story highlights the importance of locating high-quality sources of germplasm for establishing cultivated populations for the drug trade. The Dutch were fortunate in obtaining Ledger's *C. calisaya* seeds, while British and German entrepreneurs were less fortunate in that they obtained seeds from lower yielding species. The phenomenon of genetic variation for yield of desired medicinal compounds is relatively well established for many other drug plant species besides cinchona. Geographic populations of some species may be devoid of active constituents, while other populations may be highly valued. As an example, Taiwan populations of *Tripterygium wilfordii* have provided the source of tripdiolide, an active anticancer compound recently screened in the NCI program. In contrast, samples of *T. wilfordii* obtained from Hong Kong were lacking the active compound.

In addition to plants, many animal species have been directly overexploited as sources of medicinals for the folk medicine trade. In many Asian cultures, the people believe that the antlers of certain deer have a special rejuvenating, aphrodisiacal power, particularly immature antlers covered with velvet. Demand for deer products for the Chinese and Southeast Asian medicinal trade has been the major factor con-

tributing to the demise of Schomburgk's deer (*Rucervus schomburgki*) of Siam, and to the impending extinction of the white-lipped deer (*Cervus albirostris*) of the Tibetan plateau; many subspecies of the sika deer (*Cervus nippon*) of China, Japan, and East Asia; and some subspecies of red deer (*Cervus elaphus*) in Asia. Similarly, the great demand for "bezoars" or "eggs of mhorr" obtained from the endangered mhorr gazelle (*Gazella dama mhorr*) in Morocco for the Oriental medicinal trade has resulted in its near extinction.

Perhaps the most well publicized use of animals in the folk medicinal trade in recent years is the sale of rhino horn and other rhino products. Nearly all of the peoples of south and east Asia believe that various rhino products possess medicinal, magical, or religious powers. Although it is commonly believed that the Chinese and other Asian cultures use rhino horn principally as an aphrodisiac, only the penis and testicles have been widely valued for this purpose (as have the same anatomical parts of tigers and deer). The use of the horn as an aphrodisiac is restricted to certain parts of India. In China and other parts of Asia however, the horn (and to a lesser extent, the hooves) is valued for its potent fever-reducing action; it is also prescribed as an antidote for snakebite, for its cardiotonic effects, and as a treatment for boils. Many other parts of the rhino are used as well, including the skin, dried blood, bones, meat, fresh dung, and even the urine. The correlation between the specific part of the human body treated and the part of the rhino anatomy employed, however, leads one to believe that most of the prescribed uses of these rhino products are based primarily on superstition rather than on established medical grounds. In addition to the use of rhino products in Oriental medicine, the horn is also highly prized in Yemen for making special daggers called *jambias.* Rhino horn is considered superior to other types of horn for making the traditional daggers. In part, this may be attributable to the mystique of the rhino as a powerful, aggressive animal.

Rhino horn and other rhino products have been traded for a very long time; rhino trade between east Africa and Asia dates back 2,000 years. Undoubtedly, populations of the three Asian and two African species currently involved in the trade have declined gradually over the last few centuries; however, all have become endangered within relatively recent times. Total worldwide trade between 1972 and 1978 is estimated to have averaged a minimum of 7,750 kg (17,090 lb) annually, with approximately three-quarters of this trade originating in east and south Africa from the more abundant African species, the black rhinoceros (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*). Fig. 12 depicts the average wholesale value of east African rhino horn in the decades preceding the 1970's and the years following 1975. Based on the annual average from 1972-1978 and the figures provided for east African trade (the bulk of the market), the value of the Oriental horn trade in 1972 was an estimated \$225,750 (roughly \$33/kg or \$15/lb). By 1977 the average price per kilogram was about \$190/kg (\$86/lb), producing an estimated total value of nearly \$1.5 million; but in the following years, the same amount was valued at more than \$2.3 million. Prices almost doubled to \$600/kg (\$272/lb) in 1979; thus, 7,750 kg (17,090 lb) would have been worth \$4.65 million. Moreover, the estimated *retail* value of the 1979 pharmaceutical trade in Asia (almost 4,800 kg or 10,580 lb) was \$41.6 million. Thus, even though it comprised less than one-quarter of the total world trade, Asian rhino horn was the most valued of all types used in Oriental medicine; for example, by September 1979 Asian rhino horn—primarily from the Indian rhinoceros (*Rhinoceros unicornis*) and Sumatran rhinoceros (*Didermocerus

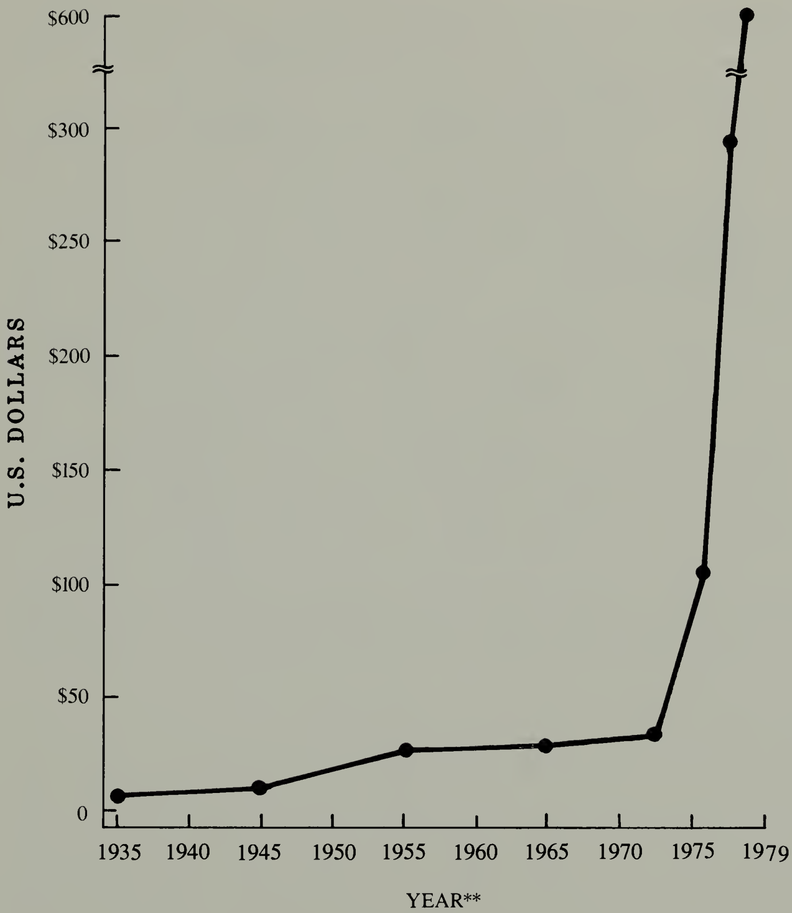


Fig. 12. Average wholesale value of one kilogram of East African rhino horn (in U.S. Dollars), 1935-1979*

*East Africa = Kenya, Tanganyika, Uganda, and after 1964, Tanzania.
**Avg. price/kg. where provided per decade until 1976. Thus, 1935 indicates the avg. price/kg. for the 1930's, 1945 indicates avg. price/kg. for the 1940's, etc.

Source: Martin, E.B. 1979 (Dec.) The international trade in rhinoceros products—A report for the World Wildlife Fund/IUCN. Nairobi, Kenya: E.B. Martin.
Obtained from TRAFFIC/World Wildlife Fund, Washington, D.C.

sumatrensis)—sold for an average *wholesale* price of more than $4,400/kg ($2,000/lb) in Asia, with Thailand averaging the lowest ($2,000/kg or $1,000/lb) and Hong Kong, where importation had become illegal in February, with the highest average price ($6,500/kg or $2,950/lb).

The dramatic trade increase of the early 1970's was attributed primarily to increased demand from Yemen for making *jambias.* Along with the tripling of oil prices during this period, Saudi Arabia experienced an oil boom, and by 1978 nearly one-sixth of the neighboring Yemeni population—almost 1 million people—regularly crossed the border to work in Saudi Arabia as unskilled laborers. Primarily as a consequence of the oil boom, the per capita income within North Yemen rose from an estimated $80 at the beginning of the decade to around $500 by 1979. In 1978, Yemenis brought an estimated $1.5 billion back to Yemen from Saudi Arabia. Many of the returning laborers began to demand rhino horn daggers; the more expensive ones with ornately carved handles encrusted with silver or gold retailed for $300-$13,000 each. Thus, despite an increased supply of rhino horns during the 1970's, demand was so great that the price began to climb precipitously.

Of course, the unfortunate consequence of this upsurge in demand was the increased hunting pressure placed on the already dwindling populations of Asian and African rhinos. In order to provide the estimated 7,750 kg (17,050 lb) annually, at least 2,500 animals were being sacrificed each year during 1972-1978, primarily from African populations. In Kenya alone, rhino populations decreased from an estimated 18,000 animals in 1969 to around only 1,500 a decade later. Presently, only an estimated 2,000 Asian rhinos (Indian, Javan, and Sumatran) and 14,000-24,000 African rhinos (black and white) still exist. Although these five species are now formally protected throughout much of their range, through 1980 perhaps as much as 50 percent of the trade in many areas was obtained via poaching from protected populations. However, even though Yemeni demand—enabled by the worldwide demand for Saudi oil—has been an important factor contributing to the recent decline of African rhino populations, most of the Asian trade and the bulk of the African horns harvested in the previous few decades were used in Oriental medicine. Since China and Japan have joined the CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), the Southeast Asian rhino horn trade has virtually ceased. The North Yemen trade continued until late 1982, when a ban was finally decreed on rhino horn imports. Between 1969-1970 and 1976-77, North Yemen officially imported 22,645 kg (49,819 lb) from East Africa (most of its imports)—some 7,850 animals (averaging 29 kg or 64 lb per animal). In previous years the trade to Yemen was insignificant; however, trade to the Orient probably claimed the lives of about 500-600 animals each year from 1930-1970. In addition to trade factors, habitat losses and persecution by humans have also contributed to the decline of rhinos.

The use of plants and animals as sources of drugs or drug precursors is not the only cause of direct extermination of resource populations. Some species have suffered from overharvesting in our attempts to provide commodities used for drug development and evaluation. If a commercially important species is already rare, especially if it has a relatively low reproductive capacity, it is particularly vulnerable when harvested under conditions of high market demand. Consider *Maytenus buchananii* (Fig. 13), an uncommon African shrub from which more than 27,215 kg (60,000 lb) of stems were procured from a game reserve in Kenya for testing in the NCI screening

Fig. 13. *Maytenus buchananii,* source of the anticancer compound maytansine, is known as "Mudziadyah" to the Digo tribe of Kenya. These people employ *Maytenus* as one component of an herbal remedy for cancer. (Illustration: Agricultural Research Service, USDA)

program. *Maytenus*, one component of an African folk remedy for cancerous conditions, was the principal source of maytansine, an active compound that at one time seemed promising as a potential treatment for pancreatic cancer. Other, more common *Maytenus* species (or their relatives, *Putterlickia* spp.) can also be used as sources of maytansine, but they typically yield much lower amounts. Thus, *M. buchananii* became the preferred source of maytansine for the NCI screening program, even though it proved difficult to locate in Tanzania, where it was previously reported as abundant. Eventually, a sizeable population was located within a forest and game reserve in the Shimba Hills of Kenya. It was from this reserve that the *Maytenus* was procured, and its availability for use in the NCI program can in part be attributed to conservation policies in Kenya. Without this readily available source of plant materials, progress in screening maytansine would have been considerably delayed, and a more thorough search (or reliance on inferior sources) would have ultimately been more costly and time-consuming. The population used primarily for the 1972 collection showed few signs of regeneration up to 1976. Thus, in order to mitigate the depletion of wild *Maytenus* populations in the reserve, a more careful effort was made in 1976 to collect the vinelike shrubs from a different Shimba Hills population.

In addition to plants, animal populations have become depleted or endangered as a result of their use as experimental subjects or animal models. A number of the nonhuman primate species once used for biomedical research are currently endangered for purposes of international trade (see Table 2); most cannot be legally obtained from the wild in their country of origin without a special permit. Aside from

harvesting for research institutions, major importing countries also demand them for pets, zoo specimens, and a very few captive breeding colonies. Moreover, within their country of origin, primate populations are also affected by habitat destruction, persecution as agricultural pests, and harvesting for food. Some of the more unusual causes of depletion include harvesting of species such as the pig-tail macaque (*Macaca nemestrina*) to serve as trained coconut pickers, and the impact of the Indochina conflicts on populations of the stumptail macaque (*Macaca arctoides*) and the endangered douc langur (*Pygathrix nemaeus*).

Although most nonhuman primate populations have suffered from the combined effects of many such causes, harvesting for biomedical research institutions has been a major factor contributing to the depletion of many populations. Notably, in the Uttar Pradesh district of India, the rhesus monkey (*Macaca mulatta*)—the most important species used in biomedical research in the United States—declined from an estimated 10-20 million individuals to around a half million. Within another district, rhesus populations declined by 90 percent within 20 years. (India formally banned trade in rhesus monkeys in March 1978 as a result of their apparent depletion, and claimed that the United States had violated contractual agreements by using the monkeys for military testing purposes.) Colombian rain forest populations of the owl monkey (*Aotus trivirgatus*) were also depleted due to U.S. demand for their use in malaria chemotherapy experiments during the late 1960's and early 1970's.

Probably the best known example of depletion of a nonhuman primate species due to demand pressure from research institutions (and zoos) is that of the chimpanzee (*Pan troglodytes*). Since infants are more tractable, and hence are preferred by harvesters and researchers alike, a very common harvesting practice was to shoot the mothers or other protective animals within a group to obtain the young. For chimpanzees, it was not uncommon for three to six adults to be killed for each infant actually exported alive. Moreover, losses during transport to importing nations were high, with as few as one of every four infant chimpanzees typically surviving the journey. As an example, consider that one supplier from Guinea, West Africa exported an average of 16 young chimpanzees each year from 1917 to 1960, thus sacrificing an estimated 3,000 to 4,000 *mother chimpanzees alone* from Guinean populations (assuming 4-6 mothers killed for every infant actually surviving export). Since the chimpanzee is a very long-lived, slow-maturing species, it does not respond well to such harvesting pressure. By extrapolation of harvesting statistics such as those noted for Guinean populations, it has been calculated that populations in Liberia and Sierra Leone would have been exterminated within only a few years if export rates of the last decade had been maintained. Indeed, all of the countries which provided information about the conservation status of this species during the late 1970's noted it as "declining."

The great demand for these primates for research purposes coupled with the biological limitations on their reproductive capacity and their decreasing availability is reflected in the high prices paid for them. For example, quoted prices for one infant chimpanzee in early 1971 were $650 to the importer and $260 to the exporter. Within the importing nations, each chimp typically sold for $2,000 or more. In 1973 the assessed value per primate exported was $223 in the Sierra Leone, a major exporter of chimpanzees. Exporting nations dealing in more abundant, smaller species which breed more rapidly averaged much less per animal collected. For example, the average value per primate was $10-11 in Colombia and Peru (where primates are also

harvested for their meat), while in most Asian countries the average was $15-17 each. However, it should be noted that import and retail prices are typically much higher than export prices. And by 1980's standards the early 1970's prices quoted above are generally very low. For example, today chimpanzees can no longer be obtained legally from the wild, and the retail price of a single, captive-bred animal is $10,000 or more! Similarly, retail prices for even very common species, such as the squirrel monkey, now average at least $150 per specimen.

Although other animal species have been overcollected for biomedical research purposes, e.g., populations of the bullfrog (*Rana catesbeiana*) and leopard frog (*R. pipiens*) in the United States, the nonhuman primates are biologically so similar to humans that they will probably remain the most intensively harvested and, therefore, most vulnerable, taxonomic group. As a consequence of their biological vulnerability to overharvesting and their conservation status, a number of primate species used in biomedical research, including the chimpanzee, have been officially listed as endangered or threatened species under the U.S. Endangered Species Act of 1973 and by the IUCN.*

The Biomedical Value and Current Destruction of Tropical Environments

Tropical lands and oceans represent our most important reservoirs of medicinal gene resources. Consider only the contributions and economic value of tropical primates for biomedical research and the number of important tropical drug plants currently in use (e.g., serpent-wood, Mexican yams, strophanthus, quinine, cocaine plant, gum arabic, benzoin tree, opium poppy, Peruvian balsam, Indian plantago), and the importance of the tropics as a genetic reservoir for medicinally useful species is immediately comprehensible. Similar conclusions could be made with respect to industrial gene resources, e.g., tropical woods, oil-, resin-, and wax-producing plants (including some oil palms), and *Hevea* rubber.

Two compelling indications of the relative importance of the tropics in comparison to temperate environments can be cited. First, on a per unit area basis, there are simply more species present in the tropical regions of the globe. Patterns of species diversity for most taxonomic groups have been shown to follow latitudinal gradients, with diversity usually increasing toward the equator. Thus, even though the tropics comprise roughly one-third to two-fifths of the earth's land surface, these environments contain a disproportionately high number of the earth's species. For example, the tropics harbor probably two-thirds to three-quarters of all higher plant species, our most important source of all economic biota. (All of the tropical drug plants listed above are higher plants). Tropical habitats similarly harbor higher proportions of the major groups of animals. As an example, most venomous marine fishes are concentrated in tropical or warm waters; even the cooler deeper waters of the tropics are amazingly diverse in comparison to very favorable marine environments in temperate waters. Tetrodotoxin is one important medicinal compound originally obtained from a toxic marine fish; additionally, most of the other toxic marine animals that have been investigated pharmaceutically were obtained from warmer latitudes. A great number of warm-water, biotoxic marine animals have pro-

*International Union for the Conservation of Nature and Natural Resources.

vided substances that produce antiviral, antibiotic, antitumor, analgesic, cardiotonic, fungicidal, and other pharmacologic effects.

Second, considering intraspecific diversity patterns, latitudinal gradients appear to exist for alkaloid-bearing plants. Medicinally important plant alkaloids include: reserpine, morphine, codeine, quinine, ipecac (emetine), vinblastine and vincristine, ergonovine, cocaine, atropine, and scopolamine; most of these drug compounds are obtained primarily from tropical species. A preliminary analysis of the number of alkaloid-producing species in temperate versus tropical floras indicated that tropical areas bear almost twice as many as temperate areas. A subsequent analysis, taking into account contemporary theories of continental drift, yielded an even more striking correlation between the number of alkaloid-bearing species present within a particular region and its historical proximity to the tropics. Further analyses showed that the toxicity of alkaloids is greater and the average (mean) content of alkaloids in plant leaves is higher in tropical than temperate species. Similarly, differences among alkaloid-producing species growing at different altitudes have been observed in New Guinea; the lower in altitude (analogous to moving latitudinally toward the equator), the greater the proportion of alkaloid-containing plants. Moreover, such altitudinal and latitudinal trends in the diversity of useful medicinal compounds are not limited to plant alkaloids. For example, in a survey of *Penicillium* molds from soil samples taken from the tundra to the tropics, the percentage of species isolated which were capable of inhibiting the growth of two species of bacteria, *Staphylococcus aureus* and *Escherichia coli*, increased significantly towards the lower latitudes. And in tropical soil samples taken at different altitudes in the Rio de Janiero area, only 49 percent of the *Penicillium* molds isolated from samples taken at 2,200 m above sea level demonstrated antibiotic activity, while 72 percent of those isolated from samples taken at 1,000 m, and 73.5 percent of those from sea level samples prevented bacterial growth and reproduction. In addition, the number of penicillin species which showed antibiotic activity not only increased from north to south, but the southern antibiotic-producing species also possessed a much wider range of inhibitory action than did the active northern species. Similar trends have also been observed for antibiotic-producing bacteria.

Why do the tropics harbor most of the interspecific, and hence intraspecific, genetic diversity on earth, and therefore a disproportionate number of potentially useful gene resources? Many hypotheses have been put forward to explain this phenomenon, most of which are not mutually exclusive. Undoubtedly, one important factor has been long-term climatic and geologic changes on earth. For example, slow climatic changes created by the episodes of glacial expansions and contractions are believed to have been an important factor contributing to the highly diverse vegetation of the Amazonian region. However, within the confines of such unalterable events, ecological interactions among species, i.e., predation, competition, and parasitism, have probably further contributed to the great diversity found in the tropics. For example, one currently popular hypothesis regarding acquisition and maintenance of alkaloids and other toxic compounds is that of pest pressure. The year-round, seasonal warmth of the tropical latitudes allows plant herbivores and pathogens to be active for much longer periods of time than is possible in temperate regions. As a consequence, plants that possess mutations favoring production of toxic, protective compounds stand a much better chance of surviving to pass on such favorable mutations to their progeny. The probability of survival of offspring in-

heriting such fortunate genetic changes would similarly be enhanced—and so on. Although such processes would also occur in temperate areas, the year-round presence of a great multitude of pathogens, herbivorous insects, and other plant predators in the tropics would present more intense selection pressures and, hence, facilitate more rapid acquisition of defensive chemicals.

The Implications of Evolutionary Processes

Our picture of the ecological processes and evolutionary mechanisms responsible for the acquisition and maintenance of natural compounds of medicinal or industrial interest is far from complete. However, some experiments and studies have demonstrated the important role that plant-feeding animals play as selective agents which maintain toxic compounds in plant populations. For example, feeding experiments with snails and slugs have shown that some species selectively feed on plants which do not produce cyanogenic β-glucosides—compounds which release hydrocyanic acid gas when the stems or leaves are mechanically injured, as in the case of feeding damage. In contrast, cyanogenic genotypes of the same plant species were avoided by these molluscan herbivores. Alkaloids, probably our most important group of medicinal chemicals, have also been strongly implicated in plant defense against herbivorous animals. Alkaloid production in plants is genetically controlled, even though particular environmental factors may influence the type and quantity of alkaloids produced to some extent. Alkaloid-containing plants are known to deter sheep and other domesticated livestock, and *Colobus* monkeys and the mountain gorilla actively avoid consuming such plants. Alkaloids are capable of killing or inhibiting the growth of members representing all the major groups of plant-feeding insects. For example, they are commonly identified as the chemicals responsible for plant resistance to crop pests, e.g., potato leaves usually contain α-tomatine, an alkaloid which repels or inhibits the growth of potato leafhopper, hornworm moth larvae, and Colorado potato beetle. Alkaloids are generally reported as toxic to most nonspecialized herbivores; however, usually a few very specialized species can feed on such plants because they possess detoxification mechanisms or other means for rendering the toxic chemicals harmless. For example, intensity of predation by populations of a lupine-specialist butterfly, *Glaucopsyche lygdamus,* has been strongly correlated with the quantity and chemical diversity of alkaloids present in flowers of Colorado lupines (*Lupinus* spp.). The larvae of this species feed only on flowering stems. Within a single lupine species, plants in populations that flower early in the summer, thus risking the threat of late frosts but escaping caterpillar predation, possess low quantities of one type of alkaloid. In contrast, plants from populations that flower later and throughout the flight season of the butterflies accumulate high quantities of different types of lupanine alkaloids. The latter plant populations were therefore exposed to very intense predation, and much more individual variation among plants was observed for both total alkaloid content and the type and proportion of the different alkaloids.

Another indication of the defensive role that toxic, plant-derived chemicals may play in predator avoidance is that of the adaptive significance of these compounds when they are acquired by organisms higher in a food chain or food web. For example, cardiac glycosides chemically similar in structure to those found in digitalis

drugs are also toxic components of many milkweed species (family Asclepiadaceae). Many milkweed species serve as host plants for the larvae of the brightly colored monarch butterfly (*Danaus plexippus*), since this species is a milkweed specialist. When young, naive blue jays (*Cyanocitta cristata bromia*) are fed caterpillars that have been raised on toxic, glycoside-producing plants, a reaction similar to the severe vomiting caused by digitalis intoxication in humans in induced in the birds. On the other hand, caterpillars raised only on nontoxic milkweeds did not cause this reaction in the birds. The strong correlation observed between the dose-effect of the monarch caterpillars and the quantity of cardiac glycosides present in their host plants indicates that this milkweed specialist actually sequesters the toxic chemicals, probably for use in its own defense. The intentional or inadvertent acquisition of toxic chemicals from food plants (or food animals) by animals has become a widespread observation in studies conducted both on land and in the sea. For example, toxic marine algae, such as *Lyngbya* spp., are commonly found in stomachs of poisonous, tetraodontiform fishes, such as the puffer fish from which tetrodotoxin was first extracted. The fact that fish of the same tetraodon species harvested from different marine environments are often nontoxic has led some people to conclude that their toxicity is related to their diet and their genetic capacity to consume toxic food species and sequester the toxins without harm.

It appears that many toxic, naturally derived chemicals probably serve a defensive role in deterring predators or parasites, or an offensive role for food procurement or exclusion of competitors. The economic significance of these observations is twofold. First, the development and maintenance of medicinally (or industrially) important chemical compounds in wild populations may actually be dependent on the survival of intact natural communities, particularly those in the biotically diverse tropics. However during the last few decades, tropical deforestation and other land conversion processes have accelerated rapidly in tropical regions; similarly, many tropical coral reefs and intertidal zones have suffered from pollution and other degradative processes. Deforestation of the tropics has becóme such a serious problem that by the year 2000, many once entirely forested countries will be essentially treeless. As a consequence, many thousands—perhaps a million—tropical species now present on earth will cease to exist. Clearly, if destruction of the remaining natural communities of the earth continues unabated, an accelerating number of sources of both present and potential future drugs will be forever lost to mankind.

Second, information about the defensive or offensive role of toxic chemicals in ecological systems, and the nature of their inheritance or their acquisition through the food procurement process, will one day provide us with valuable clues as to how we can better locate and utilize poisonous, yet medicinally important chemicals. Is it merely a coincidence that most highly toxic animals, whether terrestrial or marine, possess bright coloration? Or is this widespread phenomenon actually a type of advertisement to warn potential predators that the bearer is toxic and therefore inedible? If so, narrowing our search to animals clothed in bright oranges, reds, yellows, violets, and blacks might enhance rates of discovery of pharmacologically active natural compounds. Taking this a step further, location of the specific food resources of host-specific, "warningly-colored" organisms might also lead us to novel source(s) of such desired, pharmaceutical compounds within food webs, thus further enhancing our prospects for the discovery of new medicinals. What is the role of food chain bioaccumulation of toxic compounds within natural systems, and

what is the economic importance of such accumulations to humanity? Are host-specific, herbivorous insects good bioaccumulators of toxic chemicals? If so, could they be reared to provide more concentrated sources of drug compounds than we now obtain from their host plants? As noted previously, isoxanthopterin, a compound with anticancer activity isolated from the Asian butterfly *Catopsilia crocale*, was found to be concentrated in the wings. How widespread is this type of phenomenon and what is its adaptive significance? It is known that some brightly-colored, toxic butterfly species, such as the monarch, carry the highest concentrations of plant-derived biotoxins in their wings or other parts of the exoskeleton. Is this merely a coincidence, or could it be an adaptive mechanism for conveying these toxic chemicals to exterior parts of the body—the areas most readily available to potential predators?

When plant-eating monarch larvae first encountered the milkweed toxins, they probably incurred some metabolic or energetic cost, e.g., slower growth rates, smaller adult size, or reduced viability. Since any trait which reduces the individual fitnesses of organisms in a population would be selectively disadvantageous, it seems that the reproductive or survival costs associated with genes facilitating the acquisition of such storage mechanisms would tend to be selected against within the insect population(s) that prefer toxic food plants. What counterforce of natural selection then, could account for the development of a preference for such toxic food plants in the monarch or in other butterfly populations or species? One possible mechanism is the defensive role that stored toxins may play against avian predators, e.g., the monarch-blue jay system. Laboratory studies have showed that naive (young) jays will seize their prey by the wings, carry it to a perch, and then systematically strip the insect of its wings and legs, which are seldom eaten. They then feed on the rest of the body, as long as the butterfly presented to them is nontoxic (i.e., fed on plant lacking cardiac glycosides). The first unpalatable or toxic butterfly that the bird consumes causes illness, and after such an episode, the bird learns to reject butterflies of the same or similar color patterning. In the wild, for example in the remote mountain regions of Mexico where migrating monarch butterfly populations gather to survive the winter, some native bird species have learned to detect the difference between palatable butterflies (the larvae of which presumably fed on milkweeds lacking cardiac glycosides) and unpalatable (toxic) butterflies (the larvae of which probably fed on toxic milkweeds). For example, oriole species (*Icterus* spp.) were observed rejecting the most toxic portions of the butterflies (wings and abdomen), or consuming the less toxic portions by stripping the butterflies of their abdominal exoskeleton (which contains the toxins) and feeding on the nontoxic, inner contents. In contrast, grosbeaks (*Pheucticus melanocephalus*) selectively snapped off only the abdomens of certain butterflies for consumption, dropping the remainder, or "tasted" a toxic butterfly and then released it.

Cardiac glycosides, such as digitoxin from *Digitalis,* are bitter-tasting, and very possibly serve as the aversive stimuli for foraging birds. Some field capture studies have shown that a higher proportion of the specimens of toxic or unpalatable butterfly species have beak-mark damage on their wings than do specimens of palatable nontoxic species (presumably because once tasted, the latter are consumed). This indicates that many birds may commonly forage rather indiscriminately on both types of insects, but will reject the bitter or toxic species in favor of the palatable ones. The rejected butterflies often survive, but with telltale beak-marks on their wings.

Substantial literature on butterflies documents the collection of wing-damaged specimens observed to have been attacked by birds. Do such predator-prey interactions within food chains constitute one type of ecological mechanism by which chemical compounds, particularly those of agricultural, medicinal, or industrial interest, are acquired and maintained in natural populations? Few studies of this phenomenon have been conducted so far, and its prevalence in nature has yet to be systematically investigated. However, the results obtained thus far are intriguing, and should not be dismissed lightly. Moreover, at the rate at which natural environments and their communities of interacting organisms are currently being destroyed, we are rapidly losing some of the most important of these systems which could be used for these studies. We are also probably losing some valuable plant and animal species that harbor medicinally or industrially useful chemicals or the genes which direct their storage or production, as well as other species that may be facilitating the acquisition or maintenance of these chemicals.

It has been hypothesized that ecological interactions between species, such as predator-prey relationships, produce a never-ending cycle or spiral of adaptations matched by counteradaptations. Most of the mechanisms involved are believed to have an underlying genetic basis. But some of those observed in higher vertebrates, e.g., Mexican birds removing monarchs' wings or selecting palatable individuals, are learned behaviors which probably have a ''cultural'' basis. In the future, will we learn to conserve and more fully study natural communities to answer many of these questions and possibly discover new and better ways of locating and using medicinal (and industrial) gene resources? Or will these natural environments and potential resources be destroyed before even the most obvious possibilities have been explored?

5

Tree Resources

Worldwide, biota contribute hundreds of billions of dollars to major industrial concerns annually. The most important features of these industrial genetic resources are their potential renewability and their capability of serving as economic substitutes for most man-made industrial raw materials. The National Academy of Sciences (NAS) 1976 Committee on Renewable Resources for Industrial Materials summarized the current economic importance and future potential of industrial genetic resources to the U.S. economy:

> Renewable resources in the form of forest and agricultural products have long been used in large quantities. . . for a wide variety of industrial purposes. Their uses for housing and other structural purposes, paper and paperboard, textiles, chemical feedstocks, and fuel constitute in the aggregate one of America's largest (industrial) sectors, and one that has continuously grown.
>
> Coal and petroleum are the remains of plants and animals accumulated over the geologic past. As we contemplate diminished and more costly supplies of these nonrenewable resources, it becomes increasingly important that we assess the current capacity of the plants and animals on the earth to produce organic materials on an annual renewable basis. . . .
>
> Society—and hence federal and state governments—should have interests in the maintenance and development of our renewable forest and agricultural raw materials since they form a great national resource that is a potential substitute for nonrenewable resources and is largely independent of foreign imports. At no time in our history has there been a greater need to expand and improve the use of the nation's renewable resources.
>
> As supply problems of the nonrenewable resources become more and more critical, the technology for substitution of renewable for nonrenewable resources to meet material needs must be available. This technology must be developed for use before the readily available reservoirs of nonrenewable resources are in short supply worldwide. . . (p.5).

Both wild and genetically improved biota serve the industrial sector in a variety of ways, and the importance of the world's timber resources for supplying needed wood, paper, pulp, wood chemicals, and other wood-based products cannot be overemphasized. In 1978 the World Bank placed the total worldwide value of such forest products at more than $115 billion annually. In the United States, more than 95 per-

cent of the domestic supply of all renewable industrial raw materials is still obtained from forest products. Our industrial dependence on renewable forest resources underscores their value as strategic resources—resources that must be stockpiled in the event of a national emergency. Most of this productivity is derived from wild trees, but genetically improved tree species also contribute to annual timber productivity. In addition to supplying forest products for strictly industrial purposes, woody plants are important sources of wood and charcoal for fuel, especially for home cooking and heating purposes. Nitrogen-fixing trees, such as *Leucaena leucocephala,* can be employed to increase wood production in heavily deforested regions of the developing tropics, while simultaneously providing needed fertilizer and animal forage.

In addition, woody plants are being investigated as sources of timbers resistant to wood-destroying organisms, as candidate species for the reclamation of coal mine spoils or for controlling soil erosion, as pollution-tolerant ornamentals, and for a variety of other useful roles. The continuing discovery and genetic improvement of unusual shrubs, trees, and other ornamentals provides us with an array of beautiful or unique flora, many of which simultaneously bear edible fruits and inhibit soil erosion. However, private and commercial collecting of plants for ornamental purposes is the major threat to the survival of plant species next to habitat alterations and introductions of exotic predators. Conservation of rare ornamental or other plant species is not merely an exercise of academic interest. More than 100 of the genera that contain threatened or endangered U.S. species also contain species that were once used as sources of food by North American Indians; and the number of genera which harbor medicinally or industrially useful species as well as one or more endangered U.S. species has not yet been investigated.

Timber Products

The cell walls of woody or fibrous plants still provide our major sources of shelter, clothing, and fuel:

> The non-living supportive walls of plant cells have been useful to man from the beginning of his history. They were the main source of fuel, shelter, weaponry, tools, and fiber in early cultures, and to a great extent have remained so into the modern day. Civilization could hardly have arisen without the structural contributions from woody plants, at a time when metallurgy was in its infancy. In many parts of the world people still depend upon the forest for fuel, housing, and income...(Schery, 1972, p. 27).

Trees, economically referred to as timber, provide the greatest concentrations of woody (lignified) cell wall material. Wild forests are our most abundant source, since the great bulk of the world timber supply is still extracted from unimproved, wild stands. Today, as in the past, forested lands are important national assets which greatly influence the long-term welfare of nations. Global and national estimates of the value of forest products provide useful indicators of the economic importance of extraction industries based on exploitation of wild forest species (and the few cultivated populations). Although part of the contribution to economic productivity is provided by labor and capital inputs, these latter inputs would be unnecessary if not for the availability of trees and the survival of their forest ecosystems. From this perspective, the value of primary forest products must be considered as dependent

on and therefore synonymous with the value of the wild resources (and the cultivated ones derived from these) from which they were originally extracted.

The total annual value of primary forest products now exceeds $115 billion; most of this productivity is used locally, and therefore contributes to the economic welfare of the harvesting nations. However, in recent years world trade in forest products has increased dramatically. Annual trade volume increased at a compound rate over 13 percent from 1961-1974, reaching $30 billion. Moreover, the forest export industry of the less-developed nations grew even more rapidly, at a compound interest rate of 16 percent, rising from only $0.5 billion in 1961 to nearly $4 billion by 1975. Exports of tropical hardwoods alone trebled from 1962-1972, and by 1974 they accounted for 16 percent of the total world trade in wood products. Trade in hardwood plywood from the tropics similarly soared between 1962 and 1971—by a 400 percent increase, recently providing as much as 30 percent of the total world plywood trade. In addition to their direct monetary value, the timber extraction, processing, and retailing industries provide jobs and income for a multitude of the world's people.

Domestic U.S. timber production is an essential component of the American industrial economy. Forest products account for approximately 96 percent of the entire U.S. domestic supply of renewable industrial raw materials (on a percent weight basis). In recent years, the timber industry has employed almost as many people as the farming industry, directly accounting for at least 3-4 percent of our national income. In 1970 the delivered value of our timber resources amounted to more than $4.2 billion—the monetary value of timber after harvesting but before primary processing. The bulk of this productivity was obtained from privately owned lands, most of which are managed primarily for extraction of forest products. For example, very little of the southeastern coniferous forests are publicly owned. Most of these private lands were thoroughly cut over in the past, yet today they are managed on a more sustained-yield basis for small timber production for pulpwood. They still bring about $1 billion into the regional economy each year. In recent years, the publicly owned national forests, especially those located in the Pacific Northwest, have played a greater role in U.S. timber production. They have yielded annual cash revenues of $400-500 million for timber, despite their simultaneous management for other consumer and civilization-supporting uses, including wilderness and wildlife reserves, watershed maintenance, and outdoor recreation. Moreover, the national forests will probably increase in economic importance within the near future. Even though these areas currently comprise only 18 percent of all U.S. commercial forests, the only sizeable old growth and virgin timber stands remaining in our country lie in the far West. National forests currently harbor more than half of the standing softwood sawtimber there, as well as a large proportion of our hardwood timber.

Worldwide more than 1 billion m^3 (3.3 billion ft^3) of wood is currently used each year for industrial purposes. In the United States, as in most of the technologically advanced nations, timber is used primarily as an industrial raw material. Structural uses of forest products, e.g., sawlogs for lumber, have tended to dominate the market; second, but rapidly increasing in importance, is production of wood fiber or woodpulp for paper and paperboard. Our versatile timber resources have also been employed for a multitude of other purposes. These include: panels and veneers; plywood, particle board, and fiber board; posts, poles, pilings, and mine timbers; fuelwood and charcoal; cork and Christmas trees; and many extractives or wood ex-

udates, such as tannins, resins, oils, and dyes. Wood chemicals, such as rayon and other cellulose derivatives, can serve as economic substitutes for practically any available petrochemical. Recently, it has even been observed that tree bark, long considered useless and therefore a common pollutant of waterways, can be employed for a variety of uses including direct combustion to provide energy. In addition, trees are valuable for ornamental purposes and recreation. However, in the future, the principal economic contribution of both wild and genetically improved forest stocks will continue to be industrially oriented within the more technologically developed nations.

In addition to consideration of the major uses of forest products in industrialized nations, it is important to mention the contributions of especially valuable or high-quality forest resources. When considered only on a percent usage basis, the perceived value of unique or rare forest resources and their derived products might seem insignificant. But in reality, their true economic value may be very great, or they may be indispensible for the manufacture of specialty items or for certain critical industrial uses. For example, ever since colonial times the North American black walnut, *Juglans nigra* (Fig. 1), has remained the premier U.S. hardwood for interior paneling, cabinetry, and fine furniture. Because it is still in great demand, the recent depletion and scarcity of commercial-size walnut trees has facilitated dramatic price increases. Thus, despite the negligible overall contribution to our national income from exploitation of walnut trees, prime-size black walnut has recently commanded prices of up to $1,600-2,500 for 1,000 board feet (depending on the quality and diameter of the log). One mature stand of 18 trees recently sold for $80,000, with a single tree bringing $30,000 alone. Other high-quality American hardwood species suitable for making veneer, fine paneling, and furniture include maple (*Acer* spp.), black cherry (*Prunus serotina*), and white oak (*Quercus alba*). Virgin or mature (old-growth) stands of hardwood species contribute less to the short-term biological, and hence economic, productivity of forests than new-growth stands. But they are still necessary for the production of high-quality timber resources and will remain important for the highest-grade uses of timber.

The great economic value and special uses of little-used but high-quality timber resources is also exemplified by the U.S. demand for tropical hardwoods. Even though these imports currently account for less than 2 percent of the total U.S. consumption of forest products each year, they have averaged $430 million annually from 1974-1978. The value of U.S. hardwood imports from the tropics reached $682 million in 1978. Table 1 lists some of the more valuable or unique tropical woods currently in commercial use, and their native distribution(s). Unless noted otherwise, most of these species are used in the construction and furniture industries. Thus, they are principally used for lumber, custom flooring, fine paneling, and veneers and veneer plywood for making fine furniture and cabinets. The heartwood color or special qualities of some of these, however, has made them especially prized for making certain specialty items, e.g., French rosewood (from Madagascar) for traditional French furniture, teak (from Indo-Malaysia) for making Danish modern pieces, koa (from Hawaii) for making ukeleles, and some of the rosewoods and padauks for fine musical instruments. A few are used almost exclusively for the manufacture of certain items; for example, lemonwood (from Latin America and Cuba) is used extensively in the manufacture of archery bows, tool handles, fishing rods, and textile manufacturing items. Others have critical industrial applications be-

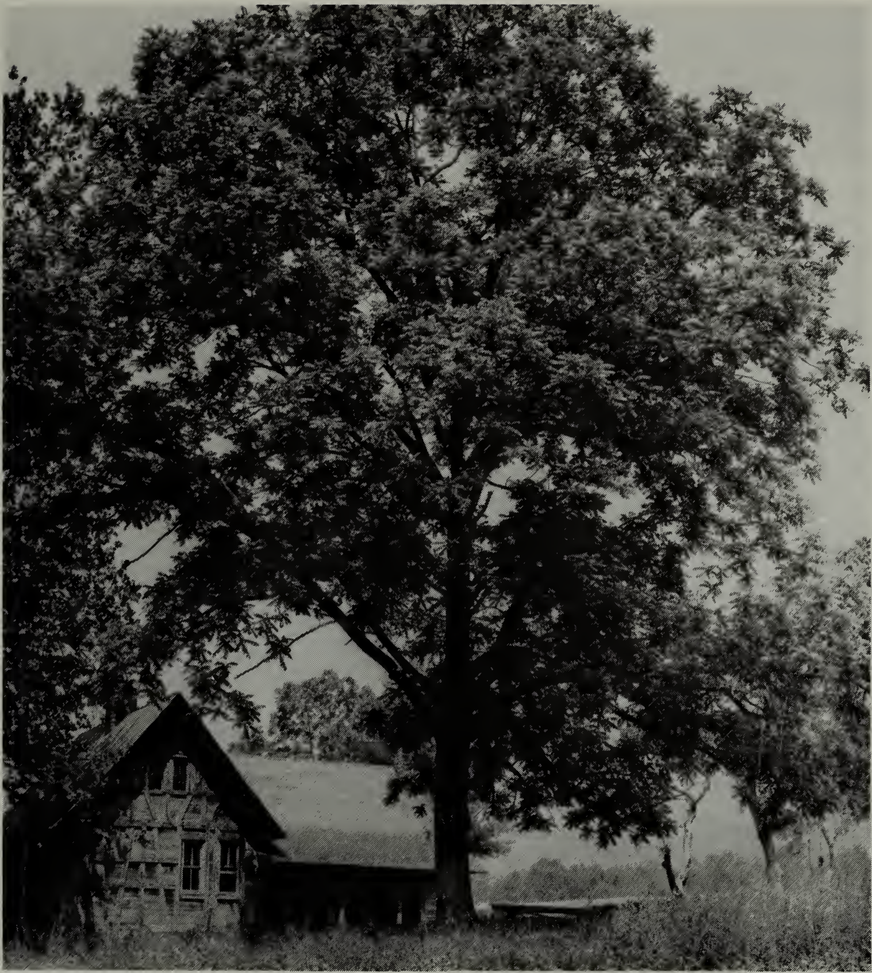


Fig. 1. The black walnut *(Juglans nigra),* a premier hardwood species of the United States since colonial times, is still prized today for making fine furniture, paneling, flooring, and cabinetry. (Photo: U.S. Forest Service, USDA)

cause they are naturally resistant to termites, insects, marine borers, or decay fungi. Naturally resistant hardwood species are highly valued for construction of ships, docks, and other coastal or marine structures for U.S. naval operations. One of the best known woods of tropical America, lignum vitae (*Guaiacum* spp.), was recently evaluated for decay and termite resistance. It was one of the only woods that lasted 158 months of terrestrial exposure to wood-destroying organisms. The natural resistance and self-lubricating qualities of this very dense tropical wood have made it one of the most important raw materials for making durable propeller-shaft bushing blocks and bearings for ocean-going vessels. In recent years, *Guaiacum sanctum* has

TABLE 1. Some Commercially Important Tropical Timber Trees

Family/Species	Native Distribution	Notes: Heartwood Color/Uses* (Resistance**)
Gymnosperms:		
Araucariaceae		
Araucaria spp. Hoop-pine	Australia; New Guinea; New Caledonia	Light yellow-brown; for pulp, light construction, paper; furniture.
Pinaceae		
Pinus caribaea Caribbean pine	Central America, Cuba, & Bahamas	Gold to red-brown; for construction, plywood, pulp, & paper.
Angiosperms:		
Anacardiaceae		
Astronium graveolens Goncalo alves	Mexico to South America	Russet, orange, or red-brown with brown streaks. (F/T)
Bombaceae		
Ochroma pyramidale (O. lagopus) Balsa	Tropical America	Sapwood (white to oatmeal) = most of commercial timber; for insulation, floats, surgical splints, & toys.
Boraginaceae		
Cordia spp. Bocote; Louro pardo	West Indies: Central America to Brazil	Tobacco to red-brown with irregular dark, brown-black streaks. (F/T)
Casuarinaceae		
Casuarina spp. Casuarina; she-oak	Tropical India to Polynesia; Australia	Lt. red to red-brown; for timber, pulp, charcoal, & firewood.
Combretaceae		
Terminalia tomentosa East Indian laurel	India & Burma	Lt. to dark brown figured with darker streaks.
Ebenaceae		
Diospyros spp. Ebony	Equatorial Africa, Indo-Malaysia	Jet black, black-brown, or streaked (light to medium brown). (T)
Lauraceae		
Cinnamomum camphora Camphorwood	Southeast Asia	Yellow, olive, orange to red-brown, to red, with camphor or anise scent. (I)
Ocotea rodiaei Greenheart	South America (northern)	Blackish to olive-green. (F/MB/T)
Persea spp. Lingue; canela-rosa	Tropical America	Reddish, pinkish, or brown.
Leguminosae/Fabaceae		
Acacia koa Koa	Hawaiian Islands	Golden brown with dark brown streaks; for veneer, furniture, & ukeleles.
Acacia melanoxylon Australian blackwood	Eastern Australia	Golden to dark brown with darker streaks.

TABLE 1. Continued

Family/Species	Native Distribution	Notes: Heartwood Color/Uses* (Resistance**)
Albizia spp. Albizzia; kokko	Tropical Asia and tropical Africa	Golden yellow, lt. to dark brown—tinged or streaked; *A. falcataria* = one of fastest growing hardwoods.
Copaifera spp. Capaiba	Panama to Paraguay	Red-brown streaked or with coppery hue; timber & gum (resin). (F/I/T)
Dalbergia cearensis Brazilian kingwood	Ceara, Brazil	Brown with thin streaks of violet or black.
Dalbergia greveana French rosewood	Western Madagascar	Rose-pink to purple-brown with dark red lines. (Now very rare)
Dalbergia latifolia Indian rosewood	Indian peninsula	Gold-brown to rose or purple-brown with streaks.
Dalbergia nigra Brazilian rosewood	Coastal Brazil	Brown, red, or violet with black streaks. (F/T)
Dalbergia retusa Cocobolo (rosewood)	Mexico to Panama	Rich orange to deep red with black stripes. (F/MB/T)
Dicorynia spp. Angelique	Surinam, French Guiana, & Brazil	Reddish-brown to gray or yellow-brown; also for marine construction. (F/MB)
Intsia spp. Ipil; merbau	East Indies	Red-brown or brown; one of most resistant timbers known. (F/T)
Microberlinia brazzavillensis Zebrawood	West Africa	Pale yellow-brown with variable patterning due to narrow, darker streaks.
Millettia laurentii Wenge	Congo, Africa	Dark brown to black with light and dark figuring. (T)
Peltogyne spp. Purpleheart	Mexico to southern Brazil	Deep purple, turning to dark brown. (F/T)
Pericopsis elata Afrormosia	West Africa	Dark brown; most valued wood in African markets. (F/T)
Pterocarpus spp. Padauk	Andaman Islands; Burma & Thailand; W. Africa	Orange-yellow, brick red, or vivid crimson with darker streaks; Vermillionwood = one of most valued.
Myrtaceae		
Eucalyptus deglupta Mindanao gum	Philippines	Lt. red to dark red-brown; a favored plantation species worldwide.
Meliaceae		
Cedrela spp. Spanish-cedar; toon	Tropical America; India to S.E. Asia	Red to rich reddish-brown. (Some spp. are termite-resistant)
Khaya spp. African mahogany	Sierra Leone, Uganda	Reddish-brown on exposure. (Moderately durable wood)
Swietenia spp. Mahogany (true)	West Indies; Mexico to Amazon basin	Rich, deep red or brown; *S. mahagoni* commercially extinct. (F/T)

TABLE 1. Continued

Family/Species	Native Distribution	Notes: Heartwood Color/Uses* (Resistance**)
Rubiaceae		
Calycophyllum candidissimum Lemonwood	Cuba; Latin America	Lt. brown to oatmeal; for archery bows, fishing rods, tool handles.
Verbenaceae		
Gmelina arborea Gmelina	India, Burma to Vietnam	Straw-yellow sometimes with pink; gen. carpentry; pulp & paper, firewood; a favored plantation species.
Tectona grandis Teak	Indo-Malaysia	Golden-yellow turning rich brown. (F/T)
Zygophyllaceae		
Guaiacum spp. Lignum vitae	West Indies; Latin America	Dark greenish-brown to black; for ship bearings, bushing blocks, propeller shafts, etc. (F/T/MB)

*Species for which *only* heartwood color is given are principally used for making fine furniture, cabinetry, and flooring, or for light construction.

**Natural resistance (moderate or high) to: decay fungi (F); insects (I); marine borers (MB); or termites (T).

Sources: Constantine, 1959; Chudnoff, 1980; NAS, 1980.

been listed on Appendix II of CITES, and trade in timber derived from this species is being monitored.

Fuel is one of the most ancient uses of wood; slightly more than a billion cubic meters is used each year throughout the world—about as much as for purely industrial purposes. Wood and wood-derived fuels produce energy cleanly and in a more environmentally harmless manner relative to most fossil fuels or nuclear power. Today the use of timber resources for the production of firewood and charcoal is centered primarily in the less technologically advanced nations where great quantities of wood are consumed daily to meet the home cooking and heating needs of their burgeoning populations. Approximately 80 percent of the households in the developing nations depend on firewood as their primary source of energy, and about 90 percent of all wood consumed in these countries is currently used for fuel purposes.

From colonial times until about 1880 the United States depended almost exclusively on fuelwood and wood-derived charcoal for energy, yet today only around 37 million m^3 (1.2 billion ft^3) of the wood harvested in America is devoted to such purposes. Over the decades, oil, gas, coal, and hydroelectric power have supplanted fuelwood for most Americans; thus, by the late 1960's, only 9 percent of our timber was used for fuelwood. Despite this dramatic decline, the United States still obtains more energy from combustion of fuelwood, bark, and other wood wastes than from nuclear power. Other industrialized nations obtain significant portions of their na-

tional energy requirements from fuelwood as well; for example, wood-derived resources presently contribute about 15 percent of Finland's energy needs, and approximately 8 percent of Sweden's. Within the near future, our current perspectives on alternative uses of wood products will be altered drastically because the global and national energy scene is rapidly changing due to depletion of fossil fuel reserves. Thus, wood for fuel and charcoal will probably again play a major role in the industrial economies of the United States and other nations. Even at present there is an expanding use of wood wastes or other plant residues for fuel. For example, during 1976, the Energy Research and Development Administration's Division of Solar Energy was supporting over $9.6 million worth of research on biomass conversion—projects designed to develop renewable biotic resources as sources of fuels and petrochemical substitutes. In spite of these research investments, biomass conversion and use of plant residues has received little attention or financial support in comparison with our massive expenditures on nuclear power; the potential for expanded production of energy from renewable plant populations remains a relatively unexplored possibility. We should therefore consider the industrial energy plantation experiments currently being conducted with oil-producing plants or with leucaena and other fast-growing trees with an eye toward our own future.

The Depletion of Timber-Producing Species

Direct extraction of timber for fuel or industrial purposes has thus far resulted in the extinction or exhaustion of few commercially valuable species; however, the economic impetus for deforestation, whether for urban-industrial or agricultural purposes, is still one of the leading causes of extinction of other valuable gene resources. In theory, wild (and man-modified) forests are renewable resources. This means that forests have the capacity to provide continuous supplies of wood for both industrial and domestic purposes; moreover, if wild stands are properly managed, they can provide wood as well as maintain valuable, renewable stocks of edible, medicinal, or other industrial resource species. However, since very ancient times, a great number of the world's forests have been exploited as nonrenewable resources, without thought of their potential as renewable sources of economic commodities. Many timber or fuelwood species are severely depleted in comparison with their vast former distribution, or are now endangered or commercially extinct. Examples include some populations of West Indies mahogany (*Swietenia mahagoni*) (Fig. 2) in the Bahamas, and the once locally valuable Caoba "mahogany" (*Persea theobromifolia*) of the Los Rios province of Ecuador. The latter species is a relative of the avocado (*P. americana*) and lingue (*P. lingue*), a valuable tropical hardwood species.

Another notable example is the Lebanese cedar (*Cedrus libani*) (Fig. 3); Lebanese cedar forests once covered nearly a half million hectares (1 million acres) of Lebanon. The beautiful, fragrant, and remarkably durable wood of this cedar species has been a favorite for all types of construction since ancient times. Yet today, after 50 centuries of exploitative and abusive cutting, only a few scattered remnants of the once vast cedar forests remain in the Lebanon mountains. A distantly related species, the Spanish cedar (*Cedrula odorato*) is similarly very rare now except in inaccessible places. The California coast redwood (*Sequoia sempervirens*) (Fig. 4), principal source of U.S. redwood products, has become depleted in more recent

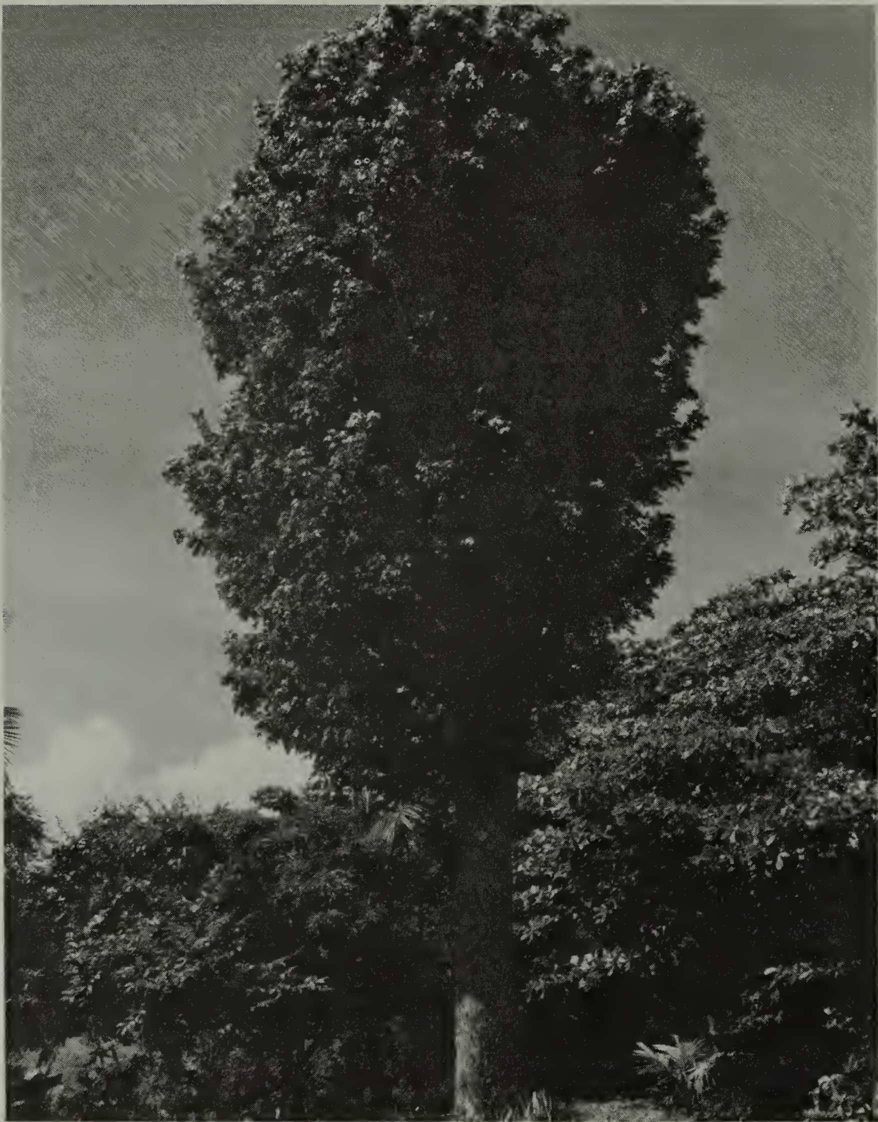


Fig. 2. A West Indies mahogany tree *(Swietenia mahagoni).* One of two commercially important mahoganies in the Americas, this species was first harvested for the lumber export trade to Spain during the 16th century and to England during the 17th century. Master wood-craftsmen developed new furniture styles designed specifically for its use, and mahogany strongly influenced the development of the Chippendale, Adam, Sheraton, and Hepplewhite styles of furniture design in England, and the Duncan Phyfe and other traditional American styles in the colonies. However, by 1735 the once abundant coastal stands in Jamaica had been thoroughly depleted. The trade shifted gradually to Cuban populations, and to exploitation of Honduras mahogany on the east coast of Central America. Today Jamaican mahogany remains difficult to obtain, and Cuban mahogany has been banned from export since 1947. (Photo: U.S. Forest Service, USDA)

Fig. 3. A Lebanese cedar tree *(Cedrus libani)* in the late 1800's. After fifty centuries of exploitation, only a few isolated stands still exist. (Photo: Gifford Pinchot, U.S. Forest Service, USDA)

times. Although the Yurok Indians of northern California once used the timber and bark of this species for construction, it was not widely exploited for timber until the Gold Rush of the late 1840's. Today only 1,470 km^2 (911 mi^2)—less than one-sixth of the original acreage—exists as virgin, old-growth timber. At least 15 percent of the original coast redwood forests have disappeared entirely; and very little of the privately owned virgin forests are expected to remain by the year 2000. Likewise, the Chilean false larch (*Fitzroya cupressoides*) of Chile and Argentina has become depleted due to commercial overexploitation during the last few centuries. This species has been commercially important since 1600 because of its great durability and natural resistance to wood-destroying organisms. It was heavily logged during the 17th, 18th, and 19th centuries, and was very scarce in the more accessible regions by 1900. However, extraction from more remote populations has continued since then, and during the 1960's it still contributed 6 percent of Chile's lumber production and 11 percent of the value of Chile's lumber export trade. The species is currently threatened with extinction, in great part due to the pressure of foreign demand for the lumber and the recent influx of foreign capital to support further logging operations. It is now protected by both the U.S. Endangered Species Act and CITES.

Another commercially important but endangered timber species, the Guatemalan fir (*Abies guatemalensis*) reaches a height of 45 m (148 ft.). Like the Chilean false larch, it is protected by both CITES and the U.S. Endangered Species

Fig. 4. California coast redwoods *(Sequoia sempervirens)* in Redwood National Park, California. (Photo: L.R. Lawlor)

Act. It has been used for lumber and fuelwood since Mayan times, and after 1524 it was extensively exploited by the Spanish for construction of administrative towns. Up until the 19th century, however, it was still one of the most common trees in the western Guatemalan highlands, and until the 1940's it was still abundant in certain areas. But by 1958, everywhere in the country except on protected government lands Guatemalan fir populations had been virtually eliminated for fuel, lumber and Christmas trees. Since 1964 the only source of energy for home use for at least 85 percent of the Guatemalan people has been firewood, and most of the people live at 1,700-2,700 m (5,575-8,860 ft) in the highlands, immediately below the elevations where the remaining populations of Guatemalan fir still exist. The survival of the remnant populations of this fir species, as well as many other conifers in the high-

lands, is currently a source of concern to both foresters and conservationists alike. The coniferous tree resources of highland Guatemala are unusually diverse, and more conifer species exist there than in any other region of equally low latitude in the world. Moreover, even though there are many economically valuable species of fir (*Abies*) trees in the world, the endangered Guatemalan fir is considered especially unique and valuable because it occurs farther south than any other fir species, and the same observation has been made with respect to some other Guatemalan conifers. Because they exist on the geographical and evolutionary frontier of the genus *Abies*, the remaining Guatemalan fir populations collectively represent a unique gene pool resource—a species that is well adapted to highland environments in the tropics. The problems of tropical deforestation are acute in hilly or mountainous regions, where many areas are now essentially treeless. Thus, if it is allowed to survive, the Guatemalan fir might prove to be a valuable firewood species for high altitude areas in the tropics. Individual trees have only rarely been recorded below 1,800 m (5,905 ft). The species ranges primarily from 2,700-3,500 m (8,860-11,485 ft), and is found as high as 4,000 m (13,125 ft) in some parts of Central America! In contrast, 3,000 m (9,845 ft) is the highest, and below 2,000 m (6,560 ft) the most common elevation for the natural distribution of all of the nine fuelwood species suggested for use in tropical highlands in the 1980 NAS report on firewood crops. Thus, the impending loss of this unique firewood and timber species would be most unfortunate. In addition to this species, there are other valuable, rare or common conifers adapted to the high altitudes of the Guatemalan highlands; examples include *Pinus ayacahuite,* a bark beetle-resistant pine which is the most highly valued pine tree in the country; *Juniperus standleyi,* an important firewood and lumber species; and *Taxus globosa,* a rare tannin-producing species which is the only yew species found south of the United States.

In many areas of the world where large-scale deforestation has already taken place, virtually every wood- or oil-bearing plant species is now valued as a fuel resource. In these regions, the depletion of preferred firewood species has generally led to increased exploitation of less accessible species or inferior sources. For example, consider the now firewood-scarce regions of the Andes. With the depletion of more accessible firewood stocks, collectors with trucks are now making regular forays to remote populations of the tola bush (*Lepidophyllum quadrangulare*), which were once considered inaccessible. After the tola bushes are harvested, they are sent by railway to La Paz and other cities as well as to treeless regions 350 miles north where municipal laws now prohibit the felling of any fuelwood species. As a consequence, tola bushes are now being cleaned out too rapidly for most harvested populations to recover. Moreover, in the Bolivian pampas, the areas currently covered with tola that are most in danger of denudation comprise two of the few remaining natural haunts of the wild vicuña *(Lama vicugna)*—an endangered ungulate species which bears the most valuable fleece in the world. Even nonwoody species are now being exploited extensively in parts of the Andes. Examples include the llareta or yareta (*Azorella glabra*) and the giant bromeliad (*Puya raimondi*). Llareta, a relative of parsley, is a cold- and arid-adapted plant of the high Andes; it is a very slow growing species currently being "mined" by dynamiting the funguslike, solid masses of growth which produce fuel resins. Similarly, the giant bromeliad, an important food resource for the Giant Hummingbird and other hummingbird pollinators, cannot withstand current harvesting pressures. This slow-growing, fuel-oil plant produces

the tallest flower spikes known; it is believed to require 100 years to reach maturity (about 9m or 30 ft), after which it flowers only once and then dies. It is distressing that now that the best fuel resources have been destroyed in many Andean regions and probably other firewood-scarce areas of the world, plant species ill-adapted for continual use as fuel resources are being overexploited.

In addition to the adverse economic and biological consequences inherent in the loss of entire wood-producing species, one must also consider the productivity losses associated with the elimination of valuable populations or unique germplasm resources (Fig. 5). This process is more insidious and difficult to perceive than that of extinction of an entire species, even though the consequences may not seem so distressing. The primary reason for this is that the economic potential of unique gene resources of timber trees has generally been ignored until very recently; we are only now exploring the possibilities of improving even the most commercially valuable species. Without realizing or understanding what is available, the value of such gene resources can scarcely be acknowledged; as a result, the economic consequences of their irretrievable loss cannot be ascertained. The old adage—what we don't know won't hurt us—does not apply here, for the losses to potential economic productivity which are occurring as a result of genetic erosion are robbing us and future inhabitants of the earth of the means for our livelihood and an enhanced quality of life.

Fig. 5. The last virgin stands of large white pine in Michigan were cut from 1900 to 1908. These stumps serve as a reminder of the stands that once existed in Kalkaska County. Progressive elimination of distinct populations of any timber or firewood species results in significant losses of gene pool resources. (Photo: USDA)

Some losses of important genetic materials occur inadvertently as a result of efforts to produce other commodities. As an example, pasturing of sheep at Cumbre del Aire (Totonicapán) in Guatemala is causing overgrazing of seedlings from most of the highly productive, isolated Guatemalan firs that exist on the southernmost edge of this species' present distribution. The loss of these distinct populations would be unfortunate, since the southernmost populations probably contain the most important germplasm resources availble for its development as a high altitude, firewood species for the tropics.

Most important losses of unique or valuable timber germplasm resources, however, are directly associated with logging or harvesting operations. The value and economic use potential of individual timber trees is usually easy to assess prior to harvesting. As a result, the largest trees with tall straight trunks, or those with burls or other prime parts of the tree used for veneer, are often extracted first. Thus for many timber species, the most common harvesting method has been to fell the best trees and leave only the culls (inferior trees) for reseeding or regeneration. Many timber regions of the world are now devoid of specimens of the most valuable species which could produce large timbers or fancy veneers. Selective extraction is particularly destructive of populations of tropical hardwoods, most of which are part of the primary vegetational structure of rain forests. Seeds or seedlings on the forest floor cannot outcompete established, towering vegetation in order to survive and take the place of the parent trees which have been sacrificed. Small clear-cut areas are often beneficial for regeneration of populations of such species, and these should be carefully managed for establishment of seedlings of more desired specimens. Large clear-cut areas, in contrast, are commonly invaded by less desirable timber species or noxious weeds which, once established, prevent reforestation with more economically or ecologically desirable species. Some clear-cut areas left alone for natural regeneration suffer from soil erosion, which also can decrease the regenerative capacity and productivity of tropical forests. In addition, in recent years some areas adjacent to native forests have been reseeded with inferior genotypes of economically useful species or with exotic species that are closely related to native species. The prevalence of all these forestry practices in the past has worsened the genetic condition of many economically valuable forest species, including some populations of pines (*Pinus* spp.), ebonies (*Diospyros* spp.), rosewoods (*Dalbergia* spp.), padauks (*Pterocarpus* spp.), and mahoganies (*Swietenia* spp.). The overall course of events has been summarized as follows:

> Compared to the natural condition in which half the world's land surface was in old-growth trees, and within recent centuries when fine forest clothed about half of North and South America, a third of Eurasia and a fourth of Africa—nearly 4 billion hectares all told—rather little virgin forest is left in the world. The once abundant forests of North America were rapidly and wastefully exploited progressively westward from the east coast, and only in the western belts are there relatively meager stands of large virgin timber remaining.... The forests of India are three-fourths gone, and even forests as remote as those of the Amazon valley and central Africa are being degraded by selective removal and gradual elimination of the finer, more important species.... The loss is not only of the great trees, but of all associated fauna and flora dependent upon the natural habitat. Thus not only will the virgin logs so in demand for rotary veneer and large timbers become depleted, but many other forest species (the usefulness of which may not even yet have been discovered) suffer decimation and possible extinction (Schery, 1972, pp. 142, 144).

In the years since this admonition, the logging of virgin timber areas and the

harvesting or clearing of cut-over, secondary growth forests has continued unabated. In many of the wood-producing regions of the world (including those in the western United States), trees are still harvested faster than they are replaced, making high-quality sawtimber stock scarce. Now that stocks of some of the more economically preferred timber species have become depleted, many of the woody species that were once considered useless are now being harvested or investigated for production of economic commodities such as pulpwood or low-grade lumber. The present rates of destruction of our forest gene pool resources reflect our generation's lack of concern for our future and for the welfare of future generations, not only with respect to the loss of specific gene resources or entire timber-producing species, but also for the impending loss of many job and income opportunities and some of the forest products we currently enjoy. Widespread indifference toward the conservation of our remaining forest gene pool resources offers little hope for reversal of these destructive trends within the near future.

New attitudes and perspectives are required to alter current forestry practices so that greater preservation, and therefore use, of forest gene resources can be accomplished. Forests must be managed as renewable natural resources, rather than "mined" as nonrenewable commodities. Conservation as a dynamic concept encompasses greater commitment to forest gene pool conservation as well as consideration of the consequences of forestry practices for maintenance of wildlife and breeding stocks of other economically useful species. This can, and should, be incorporated in our forest usage and management strategies. Wherever adequate protection is possible for sizeable tracts of representative forest ecosystems, they should be conserved in their natural state (*in situ*) for several reasons.

First, the seeds and pollen of many valuable forest species, in contrast with that of most temperate and many agricultural species, cannot be placed in cold storage (an *ex situ* strategy) for long periods of time and remain viable. In most cases, the lifespan of the tree itself easily surpasses that of its cold-stored pollen or seeds.

Second, by planting trees in foreign, protected areas, imminent losses of particularly valuable germplasm may be prevented; for example, this may be the only recourse for conserving genetic materials of the disappearing Guatemalan fir. However, some genes or gene combinations will inevitably be lost because of selection pressure in such new and distinctly different environments (though use of the *ex situ* mass reservoir strategy can capitalize on the beneficial uses of such selection pressures through facilitating development of locally adapted genetic strains). Moreover, removing most of a particular population or species from its native habitat may disrupt ecological relationships; these maybe vital to its own maintenance or that of other economically or ecologically important species. Although *ex situ* strategies play an essential role in the conservation of select portions of forest gene resources, *in situ* conservation remains our only strategy for maintaining the bulk of useful genetic diversity of these wild and essentially unimproved economic resources.

Third, since almost all economically important or potentially useful forest species are wild and unimproved, only the few, common plantation species, e.g., Para rubber (*Hevea*), coffee (*Coffea*), and some timber pines (*Pinus* spp.), have been investigated in any detail. In contrast, most commercially exploited forest species, especially those in the tropical latitudes, are scarcely known except taxonomically. Yet the species that have been carefully evaluated typically demonstrate striking amounts of genetic variability. In short, in contrast with agricultural genetic

resources, very little has been accomplished in terms of locating, assessing, or utilizing forest germplasm. Thus, as the 1978 NAS Committee on Germplasm Resources concluded, we should:

> Establish large wooded areas as Forest Genetic Reserves, in which seed collection only, but not logging, would be allowed and encouraged in order to maintain ancestral tree types, and to ensure a broad genetic base for future selection. Maximum genetic diversity of forest trees should be preserved, as it is impossible to predict the future needs of commercial forestry (1978, p. 98).

Genetic Improvement of Timber Species

Our use of forest genetic resources is currently in transition. In the past, our primary focus was that of merely locating and using available wild resources. This perspective inadvertently led to the depletion of the gene pool resources of many valuable timber species. Over the last few centuries, the supply of virgin and prime timber resources throughout the world has gradually diminished. Yet, the human population has continued to increase, thus intensifying demands for forest products, which in turn makes sustained yield forestry imperative. An increasing emphasis on forest plantations presently dominates forestry. Many of these plantations are stocked with improved genotypes of native species, or with exotic species which, as in the case of most major crops, often perform better in alien environments free of their common pests and diseases. Therefore, a shift in our focus is occurring; we are now turning more toward cultivating and even domesticating wild forest species. A group of the United Nations Food and Agriculture Organization and Environment Programme (FAO/UNEP) forest genetic resources experts in 1975 summarized this trend:

> ...it is increasingly recognized that the forests of the world and their resources must be conserved and managed in perpetuity, and that trees can be selected and domesticated for many purposes just as the wild forms of modern agricultural and horticultural crops have been domesticated (p. 1).

Timber Improvement Programs: Problems and Progress. Domestication or genetic improvement of wild timber species will require the same integrated approach that has been applied in agriculture. The essential steps in the domestication process include exploration and collection, screening and evaluation, conservation and, finally, utilization of available genetic resources. Forest tree breeders can tap the wealth of knowledge, information, and techniques that have been developed over decades of agricultural breeding and research. Yet in comparison with the agricultural plant improvement process, the investment costs of forest tree improvement programs are typically lower for an equivalent level of genetic improvement.

Despite these advantages, the task is more difficult and challenging for tree breeders. Whereas most agricultural plants are annuals, trees are long-lived perennials. The lengthy life cycle of most forest trees poses many difficulties; in particular, it lengthens the cycle of rotations and increases the need for long-term stand management. For example, the production and establishment of a new apple variety has been estimated to require approximately 35 years of evaluation and breeding trials; the evaluation of a new *Hevea* rubber tree clone, about 17 years. Moreover, the value of individual trees as sources of pest-resistant or high-yielding germplasm is seldom known or realized before they have reached maturity or significant size, even though their potential breeding value for certain economic traits may be discernable at an

early stage. Therefore, the screening and evaluation period for individual specimens often takes many years, and may even extend throughout the life cycle of the tree. Furthermore, once a superior specimen has been designated, one cannot transfer the chosen parent tree to an *ex situ* conservation site to facilitate further use. To compound this problem, most trees are "out-breeders," thus, their seeds are usually formed by deposition of pollen from another plant. Typically, then, only half of the desirable, heritable characteristics of a superior parent can be obtained by collecting its seeds. These considerations, coupled with the wild state of essentially all valuable forest species, highlight the reasons for the slow accumulation of our understanding of the genetics of trees. It is no surprise then, that tree improvement programs are still in their infancy.

In spite of these drawbacks, the primary inhibitions to the success of genetic conservation and improvement programs for forest species have been financial and political, rather than biological. Many of the biological problems that have accompanied the use of seed collected from wild stands can be circumvented by making grafts or clones of superior trees, by controlling pollination, or by the employment of such strategies as "roguing," the systematic removal of individual trees that exhibit less desirable qualities for heritable traits. In addition, electrophoresis can facilitate the analysis of genetic differences among individual genotypes for certain biochemical traits which underlie related economic traits. Other studies aid in testing or evaluating the performance of different clones or collections of seeds of a particular tree species. In this way, characteristics of potential use in tree improvement programs can be discovered. The Douglas fir (*Pseudotsuga menziesii*) (Fig. 6), America's supreme softwood timber species, offers an interesting example. Lab and field feeding preference studies have established that deer, hare, and other herbivores prefer for browsing some genetic strains of Douglas fir over others. Subsequent studies have demonstrated that preferred seedlings or saplings contain lower amounts of monoterpene hydrocarbons and higher amounts of chlorogenic acid. Coupled with research into the mode of inheritance of repellant compounds, these and other studies may provide tree breeders with valuable information for the eventual development of genetically improved strains of Douglas fir resistant to browsing by mammals. Likewise, similar scientific inquiries may be applied to the discovery and use of other heritable differences, both within and between species; and these will eventually enhance the success of genetic improvement programs for other economically valuable timber trees.

Over the past few decades, the exploitation of both intraspecific and interspecific genetic variation has already led to the development of improved genotypes for a number of forest species. The *Hevea* rubber tree (next chapter) has been significantly improved for higher yield and resistance to certain diseases and pests; improved cultivars of some fruit and nut trees have also been selected by man. *Cinchona* (Chapter 4) has been selected for higher yield of quinine as well as resistance to *Phytophthora* blight and other diseases.

Disease and insect resistance has been a common concern of most tree improvement programs. Our monocultural plantations stocked with long-lived trees necessitate the use of tree genotypes that can withstand the ravages of more rapidly reproducing and genetically plastic diseases and pests. A number of breeding programs for the development of disease- or pest-resistant varieties have been initiated for a great number of timber trees, and many of these have already released resistant varieties

Fig. 6. Douglas fir *(Pseudotsuga menziesii).* This premier U.S. softwood timber species often attains a height of 300 ft. Seedlings and young plants of some genetic strains of Douglas fir are preferred as browse by herbivorous animals, while young plants of other strains appear to be relatively resistant to their attack. (Photo: U.S. Forest Service, USDA)

for commercial use during the 1970's and 1980's (Table 2). The first commercially available, rust-resistant white pine (*Pinus strobus*) stocks were planted in 1974; they will be ready for thinning in 2004. This improvement will enable the trees to resist white pine blister rust (*Cronartium ribicola*), a disease which can devastate entire stands of white pine (Fig. 7). Increasing timber yields through genetic improvement has met with similar success. Tree improvement programs have also been established for the selection of other economically important traits in various timber species, including wood quality; stem quality, branching characteristics, and other traits that facilitate harvesting; increased production of oleoresins, tannins, sugar, syrup, or nectar (for honey production); and cold- or drought-resistance.

Although most of the breeding successes and genetically improved tree varieties have resulted from the exploitation of within-species diversity, sometimes achieving breeding goals by relying entirely on the use of within-species genetic variation is difficult. Dutch elm disease (*Ceratocystis ulmi*) (Figs. 8-9) has posed such a problem for American elms. Apparently, natural resistance to the deadly Dutch elm disease is extremely rare within the American elm (*Ulmus americana*), so researchers have turned to other related species, particularly Asiatic species such as *U. parvifolia* and *U. pumila* (Fig. 10) for the desirable resistance characteristics. Resistance to insect attack has also been attained through exploitation of related, resistant species; probably the best example is resistance to pine reproduction weevil in Jeffrey pine (*Pinus jeffreyi*) by crossing with the weevil-resistant species Coulter pine (*P. coulteri*); for other examples, see Table 3.

Breeding for disease- or pest-resistance, increased yields, or other heritable traits is only one strategy available for enhancing timber production. Factors to consider when deciding which strategies to use include the time scale and potential hazards and effectiveness of each, as well as labor and capital costs. Available evidence indicates that economic benefits accrue from location of genetic diversity and the development and use of genetically improved trees, whenever sufficient time and financial support has been invested in such efforts. As has been documented consistently, tree species pose no exception to the general rule that most plants have striking amounts of genetic variability. As human needs and values shift over time, new uses of genetic diversity among different tree species or genera will continue to emerge.

Economic Benefits of Genetic Improvement. Demands for industrial timber products in the United States are expected to increase by 80 percent between 1970 and 2000. Yet, supplies are projected to increase only 31 percent for softwood timber, and 66 percent for hardwood timber. Current inventories and estimates of prospective timber growth indicate that demand will far outstrip our domestic productive capacity by 1990. Although the outlook is quite favorable for the paper and pulp industries, the lumber and plywood industries are faced with a continuing decline in the quality of suitable timber. Serious supply problems are expected for mature, high quality hardwood species, such as walnut, maple, white oak, and birch. Given present levels of forest management, even mediocre quality veneer logs will be in short supply after the year 2000. Although the use of import products, particularly tropical hardwoods, is likely to increase, most of our future timber supply is expected to be provided from domestic sources.

The trees that will meet the demands of American consumers shortly after the year 2000 are currently growing in natural stands or are now being planted in mono-

TABLE 2. Some Uses of Intraspecific Genetic Diversity in Tree Improvement Programs

Species	Principal Uses	Desired Genetic Aims	Remarks
Pinus elliottii Slash pine	Fast-growing timber species; high-quality softwood; oleoresin production.	Increased timber yields; improved wood characteristics; resistance to *Cronartium fusiforme* rust; increased oleoresin yields.	Age of high-yielding genotypes in progeny tests ranged from 6-15 years in 1970 with 10-39 percent gains; selection and breeding of individual trees with desired traits; *C. fusiforme*-resistant variety available in early 1970's; progeny test for oleoresin production (1920) showed more than 100 percent increase; heritability estimates are currently available for most traits except disease resistance.
Pinus radiata Monterrey pine	Rapid-growing timber species.	Increased timber yields; resistance to disease pathogens—*Diplodea pinea* and *Dothistroma pini.*	Selection for disease resistance and yield: yield progeny tests for 11-12 year-old trees (1970) showed 14-22 percent gains in volume, and proved *D. pinea*-resistant variety made available in early 1970's.
Pinus strobus White pine	Timber production.	Resistance to white pine blister rust *(Cronartium ribicola),* and white pine weevil *(Pissodes strobi).*	Resistant trees were selected from natural populations for use in breeding program; resistant variety made available in early 1970's.
Pinus taeda Loblolly pine	Timber production.	Resistance to *Cronartium fusiforme* rust; also selected for survival, height, diameter at breast height; increased timber yields.	Discovered intraspecific variation for these traits from 1960's provenance trails; rust-resistant variety to be available in early 1990's.
Populus deltoides Eastern cottonwood	Timber production; urban ornamental and shade tree.	Resistance to *Melamspora* rust and *Septoria* leaf spot; tolerance to cottonwood leaf beetle *(Chrysomela scripta).*	Evaluation of clones taken from 36 natural *P. deltoides* stands from Mississippi River; discovery of resistant and tolerant clones.
Pseudotsuga menziesii Douglas fir	Premier American softwood timber species.	Resistance to browsing by snow-shoe hare *(Lepus americanus)* and black-tailed deer *(Odocoileus hemionus columbianus);* resistance to disease pathogen *Chermes cooleyii.*	Evaluation of selected *P. menziesii* clones for natural resistance; animal resistance determined to be strongly inherited and chiefly additive; *C. cooleyii*-resistant variety made available in early 1970's.

Sources: Cooper and Filer, 1976, 1977; Dimock, 1974; Dimock et al., 1976; Dorman and Squillace, 1974; Gerhold, Nikles (in FAO of UN, 1970); Oliveria and Cooper, 1977; Hanover, 1980.

Fig. 7. A western white pine *(Pinus strobus)* stand that has been devastated by white pine blister rust *(Cronartium ribicola).* (Photo: U.S. Forest Service, USDA)

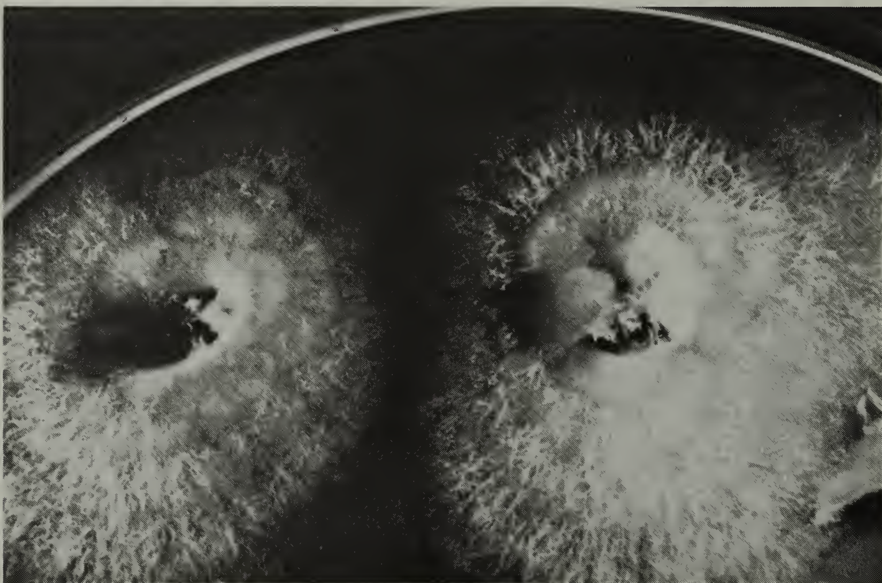


Fig. 8. Chips of elm wood infected with Dutch elm disease *(Ceratocystis ulmi)* have been placed on an agar plate in order to obtain this culture. Dutch elm disease has almost eliminated the American elm *(Ulmus americana)* from U.S. forests; the disease is carried from tree to tree by elm bark beetles. (Photo: Agricultural Research Service, USDA)

Fig. 9. A cross-section of a young American elm branch infected with Dutch elm disease. As shown by the dark rink near the edge, this disease typically causes discoloration of the spring xylem or water-conducting vessels of elm wood. (Photo: Agricultural Research Service, USDA)

Fig. 10. From 1947-1967 Massachusetts alone lost more than 150,000 American elms to Dutch elm disease. In 1967 Siberian elms, such as the one displayed by Dr. Curtis May, were imported to the United States for use in a breeding program aimed at the development of Dutch elm disease-resistant American elm hybrids. (Photo: Agricultural Research Service, USDA)

TABLE 3. Some Uses of Interspecific Genetic Diversity in Tree Improvement Programs

Species	Use	Desired Genetic Aims	Remarks
*Castanea dentata*** American chestnut	Once widely used for food (chestnuts) and tannin; timber also once employed for furniture and construction.	Resistance to chestnut blight *(Endothia parasitica)* from Asia.	Introduction of blight-resistant *Castanea* species from China and Japan; used to replace *C. dentata* and to produce resistant hybrids.
Pinus elliotti Slash pine	Timber and oleoresin production; some genotypes resistant to *Scirrhia acicola.*	Rapid growth rate and good form; resistance to *Cronartium fusiforme* rust.	Hybridization with *P. caribaea* and *P. palustris;* promising hybrids may be available soon for sites where both pathogens exist.
*Pinus jeffreyi** Jeffrey pine	Timber production.	Resistance to pine reproduction weevil *(Cylindrocopturus eatoni).*	Resistant hybrids obtained by crossing with resistant Coulter pine *(Pinus coulteri).*
Pinus radiata Monterrey pine	Rapidly growing timber species.	Drought resistance and frost hardiness.	Hybridization with *P. attenuata.*
Pinus taeda Loblolly pine	Rapidly growing timber species with good stem form.	Resistance to *Cronartium fusiforme* rust; frost hardiness.	Hybridization with *P. echinata.*
*Ulmus americana*** American elm	Favored U.S. ornamental and shade tree; timber production.	Resistance to Dutch elm disease *(Ceratocystis ulmi).*	Resistance transferred to *U. americana* as well as other susceptible American and European elms from resistant species, *U. parvifolia* (Chinese elm), *U. pumila* (Siberian elm), and *U. wallichiana.*

*Use of resistant varieties discontinued because a silvicultural control method was substituted.
**No longer economically significant, primarily due to the impact of the disease organism.
Sources: Clapper and Miller, 1949; Gerhold, Nikles (in FAO of UN, 1970); Santamour, 1974; Heybroek (in Santamour, Gerhold, and Little, 1976).

cultural plantations. More intensified management of these forest stands will be an important means of enhancing domestic timber supplies over the long-run. As mentioned above, one important management technique is genetically improved tree stocks. At present, more than 40.5 million ha (100 million acres) of our commercial forests are understocked or otherwise lacking in acceptable quality species of trees. The productivity of these and other sites could be significantly increased by planting improved genotypes, thus reducing harvesting costs, increasing timber volume yields, or facilitating tree survival in dense plantings.

In the near future, the difference between profit or loss in national and international timber markets will probably be profoundly affected by the use of genetically improved trees. Considering the length of the tree life cycle and the difficult task which faces tree breeders, tree improvement programs should be undertaken *now* if improved genotypes are to be used to enhance our domestic timber supplies in the future. Although genetic improvement programs are well advanced for a few U.S. species such as the poplars and southern pines, programs for a number of other very promising species have scarcely begun. However, it should be pointed out that reforestation projects undertaken by the public sector are saddled with high discount rates—rates that are too high to warrant such long-term investments. Discount rates are used to equate the present value of future benefits which the investor can expect to receive from his investment. The higher the discount rate, the more rapidly the projected future benefits will be discounted to an insignificant level of return. This occurs because a dollar in the hand today is worth more than the promise of a dollar returned in the future, and thus, the farther in the future one considers repayment, the less future returns are worth, relatively speaking. Socially approved discount rates of 10 percent, or even 5 percent, are so high that they can prohibit reforestation or genetic improvement projects which must be conducted on a long-term basis and which provide diffuse social benefits. On the other hand, high discount rates facilitate rapid extraction of resources, and hence the depletion of virgin and old growth forests, thus destroying gene resources that will be needed in the future. If such discounting practices in forestry continue, we may soon reach the point where there will be very little virgin timber left to extract or to use for tree improvement programs, and few reforestation projects established to take their place!

Despite these problems faced by publicly financed tree improvement programs, a number of benefit-cost analyses conducted for a variety of U.S. timber species have recently indicated that the internal rates of return (IRR's) or the marginal efficiencies of investment for genetic improvement are high enough to warrant such investments. Estimates of yield increases necessary to offset costs for the development and production of genetically improved seed range between only 0.25 and 6 percent averaging 2-4 percent—more than enough to justify the cost of establishing tree improvement programs. Even given extant genetic knowledge and preliminary field results, yield increases of improved tree genotypes of at least 5 percent are readily obtainable now, and specific studies indicate that much higher yields are possible. For example, use of improved trees of seven southern pine species can be expected to yield overall gains of 24 percent in southern timber regions. Estimates of potential volume or yield increases, and the internal rates of return on investment for each of these pine species are shown in Table 4. These figures indicate that if present timber stands in the southern regions had been stocked with superior pine, the total 1971 timber volume would have been approximately 10 billion board feet more than the

TABLE 4. Expected Percentage Gains From Use of Improved Pine Genotypes in the Southern U.S. Timber Region in 1971

Pine Species	% Increase in Present Stand Volumes*	Internal Rates of Return on Investment (%)
Loblolly	17.0 — 30.6	15.5 — 20.0
Longleaf	14.4 — 30.0	12.0 — 16.5
Sand	37.2	14.5
Shortleaf	21.8 — 28.6	11.5 — 19.0
Slash	20.8 — 42.0	16.5 — 19.5
Virginia	17.6 — 20.7	12.0 — 17.0
White	29.1 — 40.1	13.0 — 17.5

*Volume gains noted here are attributed only to the genetic superiority of improved pine genotypes, given that trees in present stands are replaced by the superior trees.

Source: Swofford and Smith, 1971.

present volume, and the annual allowable cut, 186 million board feet more than in 1971. In addition, tests with seed collected from selected white spruce have shown that the use of genetically superior stocks from Ontario, Canada yield a 35 percent better than average height growth for 9-11 year-old stands, and a 22 percent height advantage for 29-year-old stands. Moreover, progeny (seed) derived from crosses between selected white spruce trees have performed even better. In progeny tests in Michigan, the first-generation offspring of the two fastest growing parents demonstrated 63 percent more height growth. Fig. 11 depicts a progeny testing site for slash pine.

The economic benefits that accrue from tree improvement programs are not limited to immediate monetary gains: the quantity and quality of final products derived from such improved timber resources will be much higher; and the conservation benefits of initial tree improvement programs can be passed on to subsequent programs since the wild genetic resources which have been located and conserved will be available for use in future projects. Furthermore, since plant breeding is generally a cumulative, unidirectional process, improved genotypes developed now will also be available for breeding purposes later. Nor are the benefits of such programs restricted merely to economic concerns:

> Economic quantification of tree improvement benefits represents only a minimal estimate. Additional measures for crop security, cheaper processing, higher mill profits, and social benefits all would tend to tilt the balance toward even more public and private expenditures on tree improvement programs (Dutrow, 1974, p. 18).

Financial support for and conservation of a broad base of genetic variability are necessary prerequisites for the success of any forest species improvement program. These needs must be met before the forest resources management option can play a significant role in meeting future domestic timber needs.

Underexploited Woody Species

We will seek new and different uses of trees and shrubs as our environment changes in response to our changing needs and cultural values. Although it is impor-

Fig. 11. An 8-year-old progeny testing site for slash pine *(Pinus elliotti)* in Florida. In order to control sources of environmental variation, pine seeds derived from the same generic stocks are grown together in relatively small plots. Here workers are controlling the breeding of selected individuals in an attempt to obtain genetically improved slash pine seeds for establishment of fast-growing plantations. (Photo: F. Mergen, U.S. Forest Service, USDA)

tant to utilize within-species genetic variation of economically preferred species and their close relatives in breeding programs, the improvement of long-lived woody species is actually a relatively recent phenomenon. It has evolved in response to our economic focus on unique or irreplaceable biotic resource species (e.g., hevea rubber, apples) or depletion of available wild stands of such species (e.g., rare or depleted timber trees). In contrast, when we seek sources of novel products, or gene resources to meet specific societal needs, we focus our search instead on genetic differences among various species, genera, or even families of plants. For example, in comparison with other taxa, certain species or genera of trees have been found which are immune or resistant to the attacks of particular pathogens or mammalian herbivores. Others can tolerate high concentrations of certain pollutants, or can survive and reproduce under the influence of other environmental stresses that are lethal to most plant species. Even traits characteristic of certain plant families may be useful, as in the case of the nitrogen-fixing capabilities of most members of the legume

(Leguminosae/Fabaceae) family. Although leguminous species are not the only plants capable of thriving in nitrogen-poor soils, most of the members of this family benefit from symbiotic associations with nitrogen-fixing bacteria. Thus, by surveying this particular plant family, a number of multipurpose woody trees have been discovered that can survive in and aid in the improvement of severely eroded or degraded, nutrient-poor soils.

Some Alternative Uses of Woody Plant Species

Genetic differences within and among tree species are usually quite striking at all taxonomic levels of biotic organization. In general, individual trees within a population differ in their genotypic composition, and more pronounced genetic differences typically exist among groups of individuals from different populations. However, genetically-based differences characteristic of higher taxonomic levels are also of socioeconomic importance. Related but different tree or shrub species vary in their desirability as ornamental or horticultural species; in their capacity for resistance or tolerance to disease pathogens or pests; in their tolerance of various environmental stresses; and, in their usefulness for soil reclamation and conservation projects. In addition, various forest species have been singled out for their capacity for fast-growth timber production; for production of tannins, oleoresins, sugars, or other extractives or exudates; as superior nectar resources to enhance honey production; and many other special characteristics which presumably have some genetic basis.

The differential values and uses of interspecific genetic diversity which exist among species or genera of woody plants are perhaps best exemplified by comparison of various ornamental trees or shrubs. Ornamental plants are perceived as important natural features in urban landscapes, and trees in particular enhance property values. An average of 6-9 percent of the combined sale price of 60 Connecticut homes was recently attributed to good tree cover. One study of well-landscaped neighborhood parks indicated that they were responsible for 7-23 percent increases in adjacent property values. Different species of plants within the same genus, or different genera within the same family will usually differ tremendously in size, shape, growth habit, or in color, shape, and form of their flowers. One species in a genus may be a small shrub with colorful and showy flowers that is suitable for further selection and breeding as an ornamental plant. However, another related species may be a small tree with inconspicuous flowers and poor growth form. Some genera or families that contain flowering woody plants harbor many useful ornamental species, wheras others offer very few. Notable examples of plant families that have provided many woody ornamentals include Rosaceae (roses, ornamental pear, cherry, plum and apple trees, and *Spiraea*) and Ericaceae (rhododendrons, madrone, azaleas, heathers, salal, and manzanita).

Interspecific or intergeneric variation can also be quite useful in a variety of other ways. Consider the advantages of being able to substitute a closely related species for an economically valuable species which has become difficult or impossible to sustain in particular environments, as in the case of the American elm—once abundant throughout most of its former U.S. range. The most distinctive and valuable feature of this popular urban ornamental tree is its stately shape and statuesque appearance (Fig. 12). Its great height at maturity, and graceful branching patterns

Fig. 12. The great height at maturity and statuesque shape and broad crown of the American elm *(Ulmus americana)* are characteristics that have made this species valuable as an ornamental tree. (Photo: H.V. Wester)

contribute to its uniqueness among elms (family Ulmaceae). Unfortunately, natural within-species (intraspecific) resistance to Dutch elm disease, the primary cause of its decline, is apparently extremely rare. Only a single American elm clone has thus far demonstrated a useful level of resistance to this deadly pathogen, and this germplasm resource has proved susceptible to another disease, phloem necrosis. Furthermore, the American elm can be crossed with related, resistant species only with great difficulty due to differences in the basic number of chromosome sets in their respective genetic constitutions. The few moderately resistant hybrids developed to date have not exhibited the height or branching characteristics of the American elm. One researcher has suggested that the breeding and selection of *Ulmus americana* may eventually have to be abandoned unless the genetic incompatibility barrier between it and its resistant relatives can be broken, or other sources of natural intraspecific resistance can be located. Instead, an entirely different disease-resistant elm might be developed from a resistant Asian elm species, with the breeding emphasis being placed instead on selection for the aesthetic characteristics of form typical of the American elm. In fact, some hybrids between the Siberian and red elm species

already approximate these characteristics. However, these hybrids unfortunately also lack needed resistance to Dutch elm disease.

The case of the American elm emphasizes the extreme importance of natural sources of resistance to disease pathogens or predatory pests, for in this instance, lack of resistance has meant the loss of an important economic resource. In the future, it is likely that tree or shrub species desired for timber, fuel, or other purposes may be chosen primarily on the basis of their genetic resistance to the pests and diseases that might affect them in specific areas of cultivation. Various tree and shrub species differ in their natural resistance to mammalian herbivores such as seed-eating and wood-gnawing rodents. For example, New Zealand species of willows (*Salix* spp.) and poplars (*Populus* spp.) of the family Salicaceae that possess high levels of the glycoside salicin (a compound closely related to aspirin) have proved resistant to the depredations of the marsupial opossum from Australia. In soil conservation areas where opossum predation is a serious problem, resistant poplar and willow genotypes grown for reclamation purposes may be particularly useful. Likewise, species such as Douglas fir, big sagebrush, and juniper possess volatile essential oils that repel browsing animals such as deer and hare. Economically valuable timber species such as Douglas fir are likely to be preferred over more susceptible conifers for timber-producing regions where such mammals are serious pests. Similarly, different species of tropical hardwoods exhibit varying degrees of resistance to terrestrial or marine wood-destroying organisms. The heartwood of one of the most broadly resistant timber species, cocobolo or *Dalbergia retusa* (Leguminosae family), contains a protective quinone called obtusaquinone. Protective quinones are also present in another valuable tropical hardwood species, teak (*Tectona grandis*) (Fig. 13); this species is especially resistant to subterranean termites, and the compounds that confer resistance are believed to be anthraquinones. Protective chemicals have also been found in other species of pest- and pathogen-resistant tropical trees (see Table 1).

The value of termite-resistant timber species should not be underestimated. The U.S. government, which employs large quantities of wood products in both terrestrial and marine environments, is constantly seeking new methods for reducing the costs involved in repairing or replacing biologically damaged wood. In terrestrial environments, termites are responsible for much of the destruction of wood and other cellulose compounds. These insects can cause extensive damage to a wide array of materials, including wood structures, fabrics, paper, and even noncellulosic matter, e.g., asbestos, lead, asphalt, and metal foils. In recent years, it has become more difficult to obtain synthetic chemical repellents or toxic pesticides because they often produce a number of undesirable environmental side effects (e.g., human poisonings and destruction of beneficial organisms). Thus, control strategies are being directed more frequently toward the discovery of naturally resistant woods.

Recently, a study was conducted on 42 tropical African hardwoods; these species were tested in feeding trials with a particularly voracious Asian termite species to which these trees had not been exposed previously. The termite (*Coptotermes formosanus*) was collected in Louisiana where it has recently become established; it is capable of infesting woods naturally resistant to native American termite species (as would be expected for previously unexposed tree species). Twelve of the tropical species investigated showed no detectable wood damage, and after 8 weeks of exposure none of the termites had survived. Fourteen species had no ter-

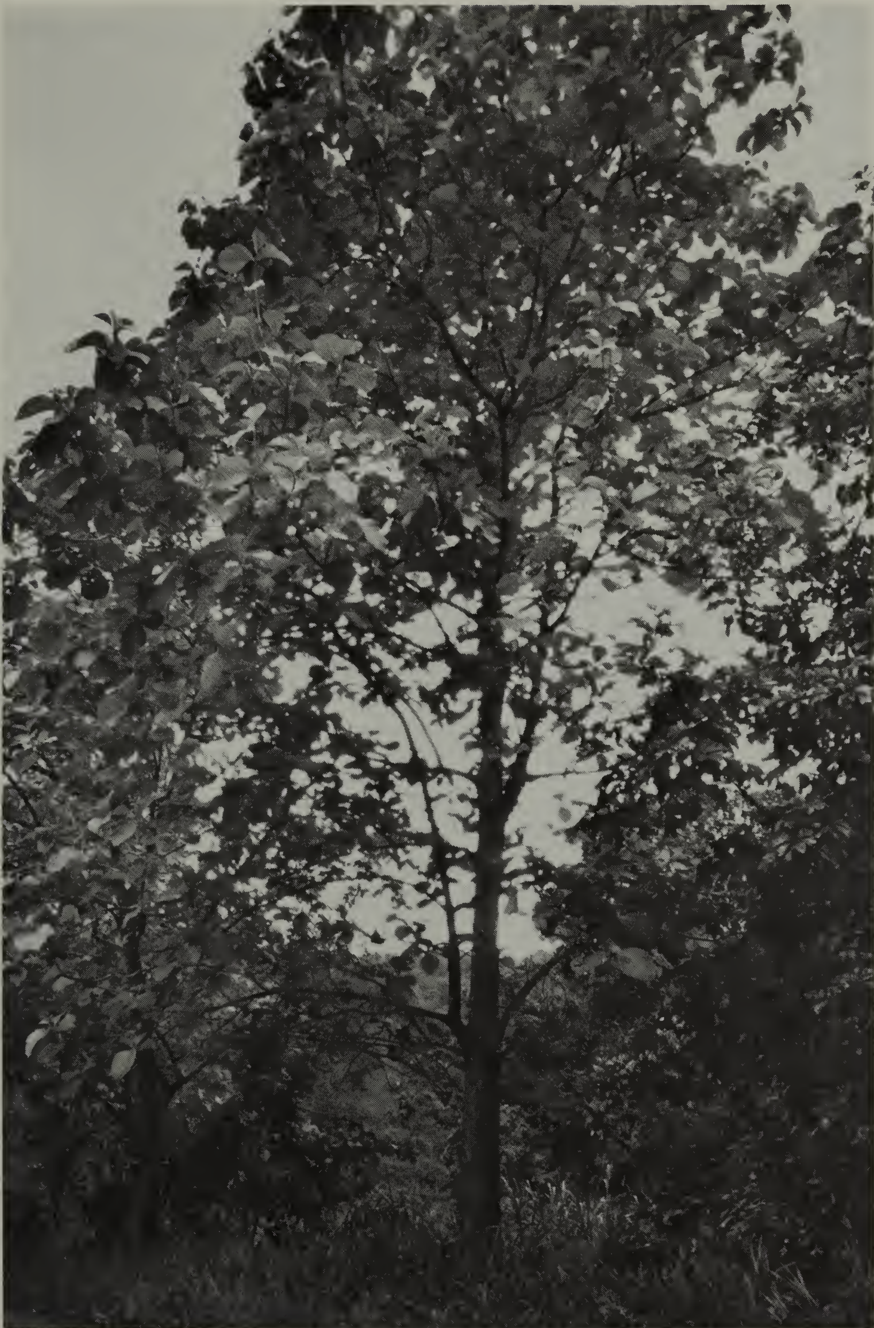


Fig. 13. Teak *(Tectona grandis)* is a fine tropical hardwood that is relatively resistant to many terrestrial wood-destroying organisms. (Photo: Agricultural Research Service, USDA)

mite survival with some wood damage; and seven species, no wood damage but some termite survival. Slash pine (*Pinus elliottii*) was used as a control, and it sustained heavy damage with an average of 91 percent termite survival. The natural resistance of the tropical species to termite attack was attributed to: physical factors, particularly wood density which reduces the ability of the termites to fragment the wood with their mouthparts; and biochemical properties, or the presence of protective chemical compounds which render the wood inedible or toxic to the termites. As the authors point out:

> These chemical constituents, generally not present in large quantities, make the wood distasteful, act as repellants, act as poisons toward the protozoan inhabitants of the termite gut, or act as systemic poisons toward the termites themselves.... The results of this study on the natural termite resistance of these 42 tropical woods suggest that all the cited mechanisms may have been operating, singly or in consort (Bultman et al., 1978, p. 3).

In addition to locating species that can counteract stresses of predation or parasitism, people of certain cultures or localities have found it useful to seek species which can survive various human-induced environmental stresses. Pollution is one such stress; in some urban-industrial areas it is such a severe problem that nearby agricultural crops are damaged (Fig. 14) or killed; some plant populations have even

Fig. 14. The leaves and flowers of a healthy alfalfa plant *(Medicago sativa)* (left) are shown in comparison with those of a plant exposed to 20 parts per million (ppm) of ozone for four hours (right). (Photo: Agricultural Research Service, USDA)

become endangered as a result of long-term pollutant exposure. For example, one U.S. species, the Torrey pine (*Pinus torreyana*) is currently endangered by smog and other air pollutants produced in the Los Angeles metropolitan area. Rather than ignoring such effects of pollutants or focusing all of our efforts on the location of tolerant species to replace disappearing species, we should consider pollution-sensitive plants as "indicator species"—species that can inform us that pollution levels are so high as to be potentially harmful to human health as well as other biota in surrounding environments. However in certain circumstances, the discovery and use of suitable ornamental species which can tolerate specific urban or industrial pollutants is a desirable aim, e.g., for inner city or industrial parks where ornamental plants are exposed to high levels of air pollutants during peak traffic or business hours, or in northern urban areas where de-icing road salts are used in winter. A number of tree species appear to be relatively resistant or tolerant to many common urban-industrial pollutants, including ozone, sulfur dioxide (SO_2), and de-icing salts. Species tolerant of high sulfur dioxide concentrations and resistant to ozone include: white fir (*Abies concolor*), sugar maple (*Acer saccharum*), western juniper (*Juniperus occidentalis*), northern white cedar (*Thuja occidentalis*), and small-leaved linden (*Tilia cordata*). Some species tolerant or resistant to all three types of pollutants are Norway maple (*Acer platanoides*), blue spruce (*Picea pungens*), and red oak (*Quercus rubra*); the black locust (*Robinia pseudoacacia*) (Fig. 15) of the legume family is particularly successful under conditions of high salt and ozone concentrations. In addition, salt-tolerant species are becoming useful in heavily irrigated arid or semi-arid areas that are building up high levels of salt in the soil. Although it is unlikely that salt-tolerant species can aid significantly in the reclamation of such areas undergoing further desertification, they still possess value as ornamentals. The special attributes of other woody plants are also being investigated for noise abatement and energy conservation purposes in metropolitan areas.

Many trees and shrubs useful for combating the environmental stresses of severely eroded or degraded habitats have been identified. Interest has increased in techniques for converting waste areas such as mine spoils into useable recreational sites. This has encouraged the discovery of woody species, as well as herbs and forbs, that can grow and reproduce under these adverse conditions. The environmental stresses associated with coal mine spoils include a bare and rocky substrate with very little organic humus or channels for percolation of water to plant roots. Under such conditions, colonizing plants must be able to tolerate very high soil surface temperatures during hot summer months. Moreover, coal mine spoils characteristically possess acid soils, low in nitrogen and available phosphorus. In addition to acid toxicity, these sites often harbor abnormally high concentrations of toxic salts, for example, copper, aluminum, iron, or manganese salts. Under such environmental circumstances, it is not surprising that most types of trees (and herbs) cannot survive or reproduce; yet some woody species, such as black locust (*R. pseudoacacia*) (Fig. 16), European black alder (*Alnus glutinosa*), larch (*Larix* spp.), and white pine (*Pinus strobus*), do survive well and maintain their growth rates.

In addition to locating species suitable for the reclamation of waste areas, we also need to discover plants that can help to control soil erosion. Soil conservation and reclamation are of crucial economic importance to industrialized food-producing nations as well as the less developed nations that are trying to feed their burgeoning human populations. In addition to the effect on present generations, the

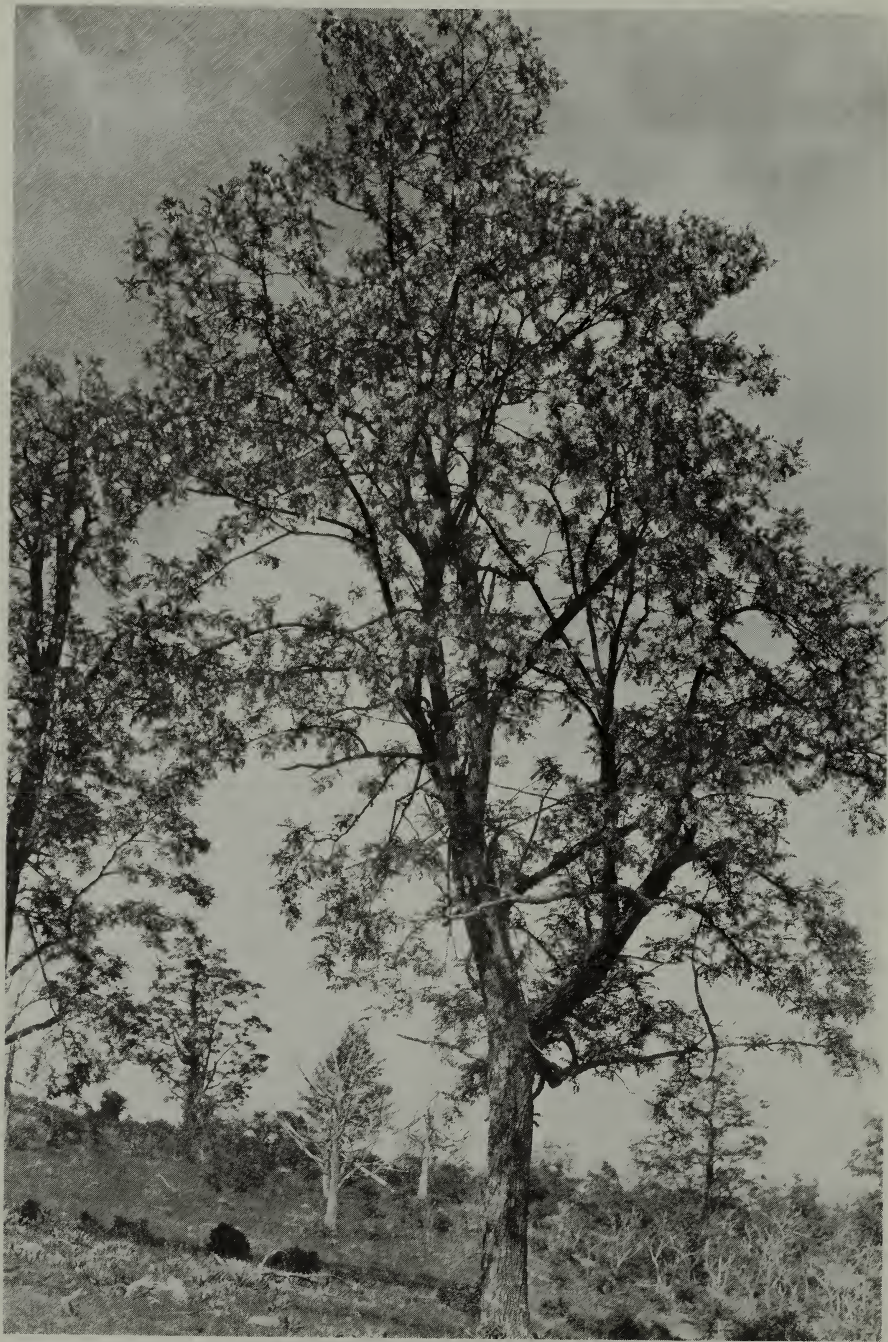


Fig. 15. The black locust *(Robinia pseudoacacia)* is one of many native U.S. trees that is tolerant to such pollutants as ozone and de-icing road salts. (Photo: Agricultural Research Service, USDA)

Fig. 16. This mine spoil in Norton, Virginia is being reclaimed through the use of nitrogen-fixing, salt-tolerant black locust. This row of locust trees (foreground) is only 2 years old, and is thriving despite the adverse soil conditions. (Photo: B.C. Venable, Soil Conservation Service, USDA)

continuous loss of productive topsoil in these areas will adversely affect the well-being and survival of future generations, just as past soil losses have contributed to the downfall of such ancient civilizations as Mesopotamia, and are now curtailing present agricultural productivity. As a result of unwise cultivation practices during the past two centuries, we have lost at least one-third of the original topsoil from useable croplands in the United States. Approximately 81 million ha (200 million acres) of once productive farmlands were ruined or severely eroded prior to 1940. Although under ordinary farming conditions topsoil can be formed at the rate of 0.6 tons/ha (1.5 tons/acre) annually (about 2.5 cm, or 1 in, every 100 years), current topsoil losses from U.S. farmlands average 4.9 tons/ha (12 tons/acre) each year with losses as high as 60 tons or more recorded in some areas. Thus, in the United States, the average rate of topsoil loss is 6-8 times the natural rate of soil formation. To the primary social cost of lost agricultural productivity must be added a variety of secondary social costs, including the pollution of water resources by soil sediments, the destruction of freshwater biota, reduction of the life span of dams and reservoirs, and the cost of additional dredging operations and additional fertilizers for impoverished farm soils. Moreover, the problem of soil erosion has been estimated to be twice as severe in some developing nations.

The role of vegetation in promoting soil conservation and countering soil erosion has been recognized since ancient times. In recent times, some technologically unsophisticated peoples as well as members of more advanced civilizations have en-

couraged vegetation in order to protect the productive capacity of the soil. One example of this in the United States was the relatively common practice of planting shelterbelts, windbreaks, fencerows, and hedgerows following the Dust Bowl days of the 1930's (Figs. 17-18). Although miles and miles of these protective vegetation lines have recently been removed, while they existed they were very effective in stabilizing

Fig. 17. Prior to the 1930's Dust Bowl days, soil conservation was not a prevalent concern in the plains of the American Midwest; as a consequence, this farmstead, like so many others, had to be abandoned because of wind erosion. (Photo: H.C. McLean, Soil Conservation Service, USDA)

soils and reducing erosion from wind and water. Furthermore, trees and forests reduce erosion caused by rapid water runoff. Climatic factors, such as humidity and rainfall, tend to limit the culture of tree species, particularly in arid and semi-arid areas. For example, most tree species do very poorly in the Dust Bowl of the southern Great Plains of the United States. However, it is possible that the present search for arid-adapted trees may lead to the discovery of some useful species for such regions. For most arid environments that are being affected by desertification however, drought-adapted grasses, herbs, and forbs should continue to provide the most protection, since these plant types do not require such continuous or copious amounts of water as trees.

Deep-rooted tree species are particularly important for stabilizing and enriching soils, since the build-up of leaf litter contributes to the organic humus content of the soil. Some arid-adapted species such as mesquite (*Prosopis* spp.) can actually "mine" groundwater with their deep root systems as well as provide fuelwood and forage for livestock. Species such as mesquite and red alder (*Alnus rubra* of the birch family) are capable of fixing atmospheric nitrogen via symbiotic bacteria, and thus can aid in replenishing the nitrogen balance of depleted soils. The nitrogen-fixing capabilities of red alder have recently been demonstrated to have a beneficial effect on the growth of Douglas fir, the premier U.S. softwood timber species. Red alder can also produce valuable hardwood timber that is a good imitation of mahogany

Fig. 18. The use of windbreaks, such as these rows of willow trees *(Salix* sp.*)* in Michigan, can significantly reduce wind and water erosion of the soil. (Photo: Soil Conservation Service, USDA)

(*Swietenia* spp.). More important however, it has such exceptional productivity—an average of 10-80 tons/ha (4-33 tons/acre) per year—that it has also been suggested as a good candidate for energy plantations to provide fuelwood for the United States and possibly some highland regions in the tropics. In the past, this potentially valuable hardwood has been systematically eradicated from certain Douglas fir stands because it was considered a pest. However, the long-standing, negative attitudes toward this species are currently changing due to its combined value as: a source of timber and fuelwood; a source of nitrogen for Douglas fir and possibly other timber species; its role in protecting Douglas fir from fire and root rot; and its value for reclaiming coal mine spoils.

Red alder is not the only nitrogen-fixing hardwood species that can be used both as a source of timber and firewood and for soil or land reclamation purposes. Probably the best known assemblage of nitrogen-fixing plants are the members of the versatile legume family (Leguminosae), the family which harbors the bulk of the firewood species discussed in the 1980 NAS report on firewood crops. Most legumes are also capable of fixing atmospheric nitrogen; and this capability is the primary reason so many of them are useful for reclamation of severely eroded, nitrogen-poor

soils. In fact, cultivation of legume crops currently contributes more nitrogen to soils worldwide than does the application of inorganic nitrogen fertilizers. Leguminous trees such as leucaena (*Leucaena leucocephala*) can be planted in the tropics for a variety of economic uses; yet they can simultaneously help to reduce soil losses and control degradation of tropical environments affected by extensive deforestation.

*Leucaena: Multipurpose Tree Crop for the Tropics**

Worldwide, the value of wood as a source of fuel is just as important as its use for purely industrial purposes. Although only about 10 percent of the North American timber harvest is used for fuel, nearly 30 percent of the European, about 75 percent of the Asian (exclusive of the Soviet Union), and 90 percent of the African and Latin American harvests are consumed solely for home cooking and heating. About 80 percent of the households in all of the developing nations depend on firewood as their primary source of energy; if desert and wood-poor regions are omitted, this figure rises to over 95 percent.

Today the real energy crisis confronting the greatest proportion of the earth's people is the daily search for firewood to cook their food and heat their homes. As the more fortunate nations of the world contemplate the future ramifications of dwindling oil and coal reserves, the poorer nations are already facing critical fuelwood shortages and the ecological and socioeconomic consequences of expanding treeless landscapes. In the most densely populated areas, human population growth is currently outstripping wood production. This situation is most critical in India and the semi-arid regions surrounding the Sahara desert in Africa. However, firewood scarcity has also become a problem in the Caribbean, Central America, and the Andes region of South America. In some areas of Pakistan, the need for firewood is so great that trees lining the streets are stripped of their bark; and although the Himalayan foothills in Nepal were once heavily wooded, today villagers must spend an entire day searching for firewood for the home stove. Only a generation ago, the same task required no more than a few hours.

Humans have already removed a large portion of the original forest cover of the earth. Nearly two-thirds of the once forested expanses of Southeast Asia, half of those of Africa, and a third in South America have been removed. The consequences of the increasing demand for fuelwood and widespread deforestation in these tropical regions are manifold. Soaring wood prices and the consequences of firewood scarcity, coupled with the petroleum crisis and scarcity of kerosene, have intensified the misery of poverty-stricken wood consumers in these areas. As a result animal manures, once used to replenish nutrient-robbed fields, are now burned as fuelwood substitutes. Over the long run, this diversion of animal fertilizers will decrease food production capabilities. Yet, for the people now inhabiting severely deforested areas, the location of fuel for cooking food, rather than enhancement of actual food production, will remain the greatest immediate challenge of the future.

The most damaging consequences of extensive deforestation are soil erosion and the host of other adverse ecological effects that sap the land's long-term production capacity, including irretrievable losses of gene resources. Large-scale development or

*All of the photographs in this section appear in a 1977 report prepared jointly by the Philippine Council for Agriculture and Resources Research and the United States National Academy of Sciences. Information on *Leucaena* in this section is excerpted primarily from this NAS report.

deforestation of humid tropical regions often leads to the establishment of economically useless, coarse grasslands. In some areas, repeated removal of living vegetation results in severe nutrient losses and, ultimately, desertification or irreversible hardening of lateritic soils to rocklike formations. In an effort to solve the problems of widespread deforestation amid growing demands for firewood, concerned scientists have been searching for species of fast-growing trees that can stabilize soils while producing good quality firewood. However, prime candidate species for reforestation and reclamation projects in the tropics must be chosen only after careful consideration of the ecological limitations of fragile tropical soils and the potential usefulness of available, native species. Species favored should contribute to, rather than deplete, the nutrient balance within the ecosystem. In addition, they should be able to outcompete invading vegetation, such as bamboos and *Imperata* or other coarse grasses, without themselves becoming noxious or aggressive pests. Thus, although such fast-growing hardwoods as *Gmelina arborea* and *Eucalyptus deglupta* have shown much promise, nitrogen-fixing species, such as many members of the legume family, should often be preferred as wood-producing alternatives for severely deforested areas.

Most higher plants cannot survive where soils lack nitrogen in the form of ammonia or nitrate. In contrast, most leguminous species benefit from a symbiotic relationship with root-nodule bacteria of the genus *Rhizobium* which can utilize nitrogen in soil air pockets. Many legumes produce so much excess nitrogen, primarily in the form of foliar protein, that when their leaves fall to the ground and decay they greatly enrich the soil around them. A number of woody legumes have been proposed as prime candidates for wood production in the tropics. These include: *Leucaena leucocephala; Albizia falcataria* and other *Albizia* spp.; *Sesbania grandiflora; Acacia mangium* and *A. auriculiformis; Dalbergia sissoo; Enterolobium cyclocarpum; Prosopis* spp.; and *Calliandra callothyrsus.*

However, *Leucaena leucocephala* (Fig. 19)—commonly called leucaena, but also leadtree or popinac in the United States and some former British colonies, koa haole in Hawaii, and bayani or giant ipil-ipil in the Philippines—has shown more promise for meeting these needs in the tropics than perhaps any other species investigated thus far. With its *Rhizobium* symbiont (Fig. 20), leucaena is capable of fixing nitrogen at the rate of more than 560 kg/ha (500 lb/acre) annually. This would be the equivalent of approximately 2,800 kg/ha (2,500 lb/acre) of ammonium sulfate fertilizer per year. In addition, under natural conditions this species is infected with a beneficial fungus that aids the plant in obtaining phosphorus and other essential nutrients.

Leucaena can provide a more or less permanent, living mulch on overgrazed, heavily deforested, or otherwise eroded terrain (Figs. 21-22). It is deep-rooted and fast-growing, and thus can quickly replace vegetation that has been lost or destroyed. Leucaena not only increases the nitrogen content of the soil, but also breaks up tightly compacted soil layers, improves water absorption, and, in the dry tropics, decreases the rate of water evaporation. It greatly reduces the erosive impact of the sun, wind, and rain. Once established, leucaena is persistent and fire resistant. Most important of all, its fallen leaves rot to form organic humus for impoverished tropical soils. For these and many other reasons, leucaena can be used by itself or with other woody vegetation in tropical reforestation projects. In Indonesia, a number of such projects have already been instituted.

Fig. 19. A fruiting branch of leucaena *(Leucaena leucocephala). Leucaena* produces drooping clusters of flat, edible pods. (Photo: N.D. Vietmeyer)

Fig. 20. A taproot of *Leucaena,* showing the root nodules that house its bacterial symbiont—*Rhizobium.* Rhizobium bacteria are capable of fixing nitrogen (N_2) present in soil air pockets. The nitrogen is converted into nitrogenous compounds that can be used directly by the plant. These compounds are eventually stored in leucaena's foliage; later the leaves fall to the ground and enrich neighboring vegetation. The foliage can also be harvested and used as an organic fertilizer. (Photo: M.J. Trinick)

Figs. 21 and 22. Situated at the entrance of Manila Bay, Corregidor Island was thoroughly bombed and denuded of vegetation by the end of World War II (1945) (above). After the war, leucaena was seeded by air, and by 1976 (below), a dense leucaena forest had become established. Although leucaena is still the dominant vegetation today, there is evidence that the original forest vegetation is slowly becoming reestablished. In this reforestation process, leucaena has played an important role in conserving and improving the fragile tropical soil, and serving as a "nurse crop" for the young forest tree seedlings. (Photos: U.S. Army and J. Black, Jr., respectively)

Because leucaena can outcompete or suppress the growth of invading grasses which would otherwise prevent natural reforestation, it may play an important role in the conservation and regeneration of tropical forests. In the Philippines, approximately 6 million ha (15 million acres) of original forestland have been transformed into essentially worthless *Imperata cylindrica* grasslands. Many other tropical forests have similarly been lost to this tenacious grass in Indonesia, Papua New Guinea, and parts of Africa and Asia (Fig. 23). *Imperata* forms a dense underground network of

Fig. 23. Mountain slopes in southern China covered with *Imperata* grass. When woody vegetation in mountainous tropical areas is burned, cut, or otherwise destroyed, essentially worthless, coarse grasses such as *Imperata cylindrica* often invade the affected areas. Such weedy species can actually prevent natural reforestation. (Photo: R. Pendleton)

roots and stems that crowds out the seedlings and saplings of desirable forest species. Removal of the grass is usually impractical and uneconomical. However, if leucaena is properly planted and carefully tended for its first few months, it will grow to dominate and eventually kill these invading grasses (Fig. 24). After the dense mat of grasses decays, seedlings of primary forest trees and other vegetation can become established. Leucaena will continue to shade and protect the young woody plants until they can grow to overtop their "nurse" plants. Once the young forest trees have become well established, the leucaena can be harvested for wood or other purposes.

In addition to its soil improvement and reforestation values, leucaena also continuously supplies a variety of useful products. Densely planted stands in the Philippines have produced higher annual yields of wood than any other species measured. Whereas other fast-growing hardwoods, such as *Gmelina, Eucalyptus, Albizia,* and *Anthocephalus,* yield annual increments of 25-37 m^3/ha (355-545 ft^3/acre), leucaena can produce 21-87 m^3/ha (300-1,250 ft^3/acre) annually. It is a medium hardwood with good machining properties—thin barked, light colored, and close grained. Wood of the Salvador-type genetic varieties possesses much commercial potential. With proper thinning and management, they will produce essentially branchless, straight

Fig. 24. Once covered by tenacious *Imperata* grass (as in Fig. 23), these slopes in the Philippines are now planted with leucaena and comprise part of a 3,000 ha (7,500 acre) energy plantation for the Mabuhay Vinyl Corporation. (Photo: M.D. Benge)

trunks that can be used for lumber, paper and wood pulp, telephone and power poles, fence posts, crop prop poles, and a host of other items. The wood of the Hawaiian-type leucaenas is more dense, however, and these strains make better sources of firewood for household or small-scale village use. Moreover, if the trees are felled near ground level, they resprout (coppice) quickly, and may be harvested repeatedly on a 5- or 6-year cycle in equatorial climates.

In the developing nations which depend primarily on wood for power, the fast-growing Salvador varieties are also prime candidates for firewood and charcoal production. These genotypes are more suitable for large-scale energy plantations which can be used for fueling food-processing facilities, electric generators, railroad locomotives, tin smelters, kilns, sawmills, and other industrial operations. Wood-derived fuels have long been used to generate electricity and steam; options for conversion of wood to fuel include pyrolysis to produce charcoal or low Btu gas, and liquefaction to provide oil and other hydrocarbons. Industries based on combustion of wood or wood-derived fuels circumvent the losses incurred during the transmission or transfer of electrical power. Wood biomass conversion is also typically less destructive in its environmental impact. There is very little or no sulfur present, and hence no production of sulfur dioxide (SO_2) air pollutants. Moreover, wood ash residues can be used as fertilizer, and harvesting of biomass does not cause extreme disorganization of soil or land resources as does extraction of oil shale or strip mining for coal. Furthermore, leucaena can be planted on land ill-suited for agriculture or other productive operations. For example, deforested hillslopes in the Philippines that had become invaded by *Imperata* grasses were recently converted into a leucaena "energy plantation." The Mabuhay Vinyl Corporation plans to use the charcoal and wood-fuel derived from leucaena for its industrial operations (Fig. 24). Two other corporations have also planted vast areas of leucaena for fuelwood, charcoal,

and stand-by electricity generation; and a Malawi sugar factory is growing a Salvador-type leucaena for steam generation.

Conversion of wood to charcoal is an essential process for many industries in petroleum-poor nations. Although much of the original biomass of the wood is lost, the charcoal has a much greater energy content and provides smokeless heat. The Hawaiian-type varieties of leucaena, which produce a very dense wood and more heat upon burning, have proved especially valuable for charcoal production. Charcoal from these genetic strains has 70 percent of the combustion value of fuel oils (7,000 cal/kg or 12,000 Btu/lb). Charcoal *per se* can be used to produce many industrial products; these include pig iron, steel and other ferroalloys, as well as calcium carbide for the ultimate production of vinyl chloride and plastics, ethylene and acetylene. The latter product is suitable for organochemical industries which lack a petroleum base. The Hawaiian strains are also particularly useful for supplying energy for cottage industries and small households. The wood or charcoal may be sold by rural people in urban areas. Because leucaena forms coppices and can survive repeated cuttings, the people can continue to use it to earn a small cash income. Thus, planting this woody legume along roadsides, in shelterbelts, and on farms or unused land surfaces throughout rural areas might provide one of the most important means of relieving firewood scarcities in the developing nations.

Leucaena can also be employed in a variety of other ways. Probably the earliest recorded use of leucaena is as a shade and nurse plant for tropical crops. It has contributed humus and nitrogen and other nutrients for a number of agricultural, medicinal, and industrial crops, including citrus, tea, cacao, coffee, pepper, vanilla, coconut, *Cinchona* (for quinine), oil palm, rubber, and seedlings of teak and other timber species. In the Philippines, valuable timber species such as teak, mahagony, and even some fast-growing leguminous hardwoods, showed 50 to 100 percent growth increases when interplanted with leucaena. Furthermore, it is a valuable ''green manure'' crop which can enhance the productivity of some crop plants. In Hawaiian field trials, leucaena meal yielded 4.3 percent nitrogen, and was capable of supporting corn yields equal to those obtained through the use of more expensive inorganic fertilizers.

Leucaena can also be used as a food and forage plant. The short, multibranched Peru-type plants yield copious amounts of highly nutritious, leafy fodder for cattle or other domestic animals and wildlife (Fig. 25). Use of leguminous forage plants like leucaena has already increased animal productivity in some areas of the tropics. The foliage possesses well balanced proportions of essential and other amino acids, and is comparable with other animal feedstocks such as alfalfa. In Indonesia and Central America, many people eat leucaena pods and leaves. However, until plant breeders are able to develop new varieties lower in the toxic alkaloid mimosine, its use for food and forage will be somewhat limited.

The presence of mimosine and its toxic effects highlight the need for genetic improvement of this multipurpose genus of trees and shrubs. When mimosine is present in sufficient quantities, it limits the palatability of this species as a human and animal food. Yet, even the mimosine can be put to use. This alkaloid typically causes hair loss when fed regularly to grazing animals or humans for an extended period of time. Sheep fed an exclusive diet of leucaena for 10 days can be easily sheared with merely the stroke of a hand. Except for making the sheep susceptible to sunburn, this depilatory method does not appear to harm them.

Fig. 25. Leucaena's fast regeneration capacity and strong, pliable, thornless branches make it an excellent shrub for tropical and sub-tropical pastures. Leucaena is highly palatable to cattle, goats, and water buffalo; these livestock species are not as susceptible to the toxic effects of the alkaloid mimosine, as are many other animals. (Photo: G. Sánchez Rodríguez)

Although unimproved leucaena genotypes are not ecologically adapted to high mountain or truly arid tropical environments where the need for firewood is often greatest, *Leucaena leucocephala,* with the genetic variability that characterizes it and its wild relatives, has a broad distribution throughout Mesoamerica (Fig. 26). Breeding programs have already been designed to develop mimosineless or low-mimosine, high-yielding forage varieties. By crossing *L. leucocephala* with *L. pulverulenta,* a species native to northern Mexico and the southern United States (especially Texas), breeders have obtained multibranched forage hybrids with less than half the normal concentration of mimosine (Fig. 27). Moreover, since the sub-tropical species (*L. pulverulenta*) typically possesses some frost resistance, cold-tolerant hybrids for tropical mountainous terrains are likely to be perfected in time (Fig. 28). The potential success of breeding programs for the development of cold- or drought-tolerant or low-mimosine content varieties of *Leucaena* has been greatly enhanced by a germplasm collecting expedition conducted early in 1978. Great emphasis is currently being placed on screening the new accessions for these characteristics. Surprisingly, the subtropical areas of Texas may provide both valuable leucaena germplasm and habitats for vegetative storage of such genetic resources. This state contains part of the northernmost distribution of *L. leucocephala,* and it harbors populations of *L. retusa* and the cold-hardy *L. pulverulenta* as well. Thus, an arboretum or other *ex situ* germplasm maintenance area situated in south Texas could further aid in the development of leucaena varieties for extending the range of adaptation of this highly useful species.

Fig. 26. *Leucaena leucocephala* originated in Mesoamerica; pre-Colombian Indians discovered its usefulness, and spread it throughout the lowland coastal regions of Mexico and Central America. Today, the 'Hawaiian' type, a very productive shrub, is still scattered throughout these coastal areas. The 'Salvador' type, a tall tree with large-sized pods (legumes), is distributed across Guatemala and southwestern Mexico, where leucaena legumes are a traditional food item. (Illustration: U.S. National Academy of Sciences)

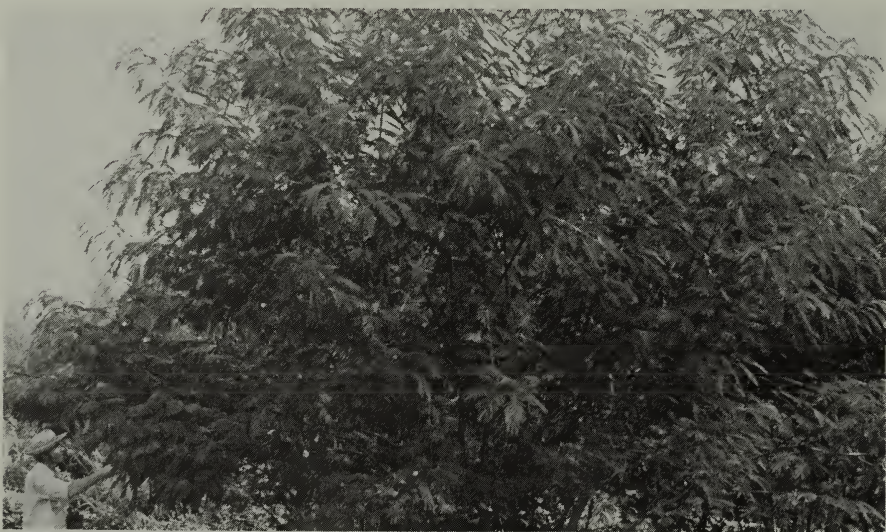


Fig. 27. This leucaena hybrid contains very little mimosine; it was produced by crossing the 'Cunningham' cultivar of *Leucaena leucocephala* with *L. pulverulenta,* a related wild species that is distributed throughout Mexico and parts of the southern United States. (Photo: W.M. Beattie)

Fig. 28. The frost-resistant *Leucaena pulverulenta* has also been used as parental stock for the development of cold-tolerant, fast-growing leucaena strains, such as this treelike *L. leucocephala* × *pulverulenta* plant at the Wailua Research Center in Hawaii which grew to a height of 12 m (40 ft) in only 4 years. At present, leucaena is not well adapted to cool tropical highlands where, in many cases, the demand for firewood is greatest. Researchers hope that useful hybrid leucaena strains can be developed for use in higher elevations in the mountainous tropics as well as in more temperate climates. (Photo: J.L. Brewbaker)

In order to realize the promise that *Leucaena* and other woody leguminous species hold for solving some of the many problems created by firewood scarcity and widespread deforestation in tropical environments, we must expand our awareness and use of available germplasm resources. Use of these must be coupled with conservation of populations of both common and threatened leucaena species and genetic strains, both *in situ* and *ex situ*. Some forms of leucaena are presently threatened in their Mexican and Central American habitats. Through adequate conservation measures, these endangered populations might one day prove valuable in our attempts to cultivate and even domesticate this multipurpose genus of trees.

6

Natural Rubber

Natural rubber is now enjoying an economic comeback and is still so valuable to industrialized nations that it is commonly stockpiled in the event of national emergencies. Today, virtually the entire world supply of natural rubber—about a third of the total rubber supply—is derived from genetically improved *Hevea brasiliensis* trees. The economic future of this valuable industrial crop may well depend on the future survival of wild *Hevea* gene pool resources in Amazonian rain forests. However, the renewed demand for natural rubber has spawned much needed research for the discovery, use, and genetic improvement of other rubber-bearing species, particularly guayule (*Parthenium argentatum*), a native American plant. An important feature of guayule is its adaptability to semi-arid environments; development and use of it and other drought-tolerant plants will enable significant expansion of arable land in the near future as well as attainment of new production options for renewable sources of rubbers and oils.

Hevea Rubber

Natural rubbers are produced by thousands of different species of plants. The use of plant-derived elastomers was first discovered by ancient American cultures; long before Columbus introduced rubber to Europe from tropical America, native American Indians from the Amazon Basin to New Mexico had made extensive use of this resilient material. For approximately three and a half centuries, the procedures involved in the use and extraction of crude rubber remained virtually unchanged by "civilized" man. Crude rubber was not widely known to people of industrialized societies until after the discovery of vulcanization by a British chemist in 1834 and an American chemist, Charles Goodyear, in 1839. The vulcanization process gave the raw material greater strength and tolerance to heat and cold, and removed much of its stickiness. Thus, this process significantly enhanced its economic potential.

Scarcely more than a century has passed since the initial introduction of the

Brazilian or Pará rubber tree (*Hevea brasiliensis*) to British plantations in the Far East. Yet, today the hevea rubber tree supports a large-scale natural rubber industry that is rapidly expanding in its scope and importance. *Hevea brasiliensis* has been called our most recently domesticated economic plant. Indeed, high-yielding and disease-resistent genotypes of this species have been developed. However, *Hevea* cannot be considered domesticated in the same sense as most economic crops, e.g., corn or wheat. Most of our economically valuable crop species are annuals which have been subjected to thousands of years of human (as well as natural) selection. In contrast, *H. brasiliensis* is a long-lived perennial, and less than a century of breeding and selection has been invested in it.

Currently, natural rubber is a strategic raw material necessary for war preparedness and other national emergencies. As an inedible crude materials import, rubber is topped by only lumber, wood pulp, and iron ore in quantity. In 1974 alone, the United States imported over $500 million worth or 719,000 tons of hevea rubber. The economic importance of natural rubber, and *Hevea* in particular, has been emphasized as follows:

> Natural rubber is now the world's most important industrial crop, finding application in a wide range of industries. Its very special niche is heavy-duty tires of the aviation and haulage industries; it is also the major component of radial ply tires for the automobile. World production is currently between 3.0 and 3.5 million tons, about 34% of total elastomer consumption. Demand for natural rubber is strong, and even more so since the oil crises of 1973 which ended the days of cheap synthetic rubbers. By 1985 the world will need about double the present output and worsening supply shortfalls are expected in the immediate years ahead. The prospects for the natural rubber industry are very bright indeed (Templeton, 1978, p. 7).

The success of rubber as an industrial raw material has been primarily due to its versatility and adaptability for a variety of industrial and domestic purposes:

> Many kinds of articles can be fabricated from rubber—hard, strong structural materials; soft, yielding, comfortable materials; conductors and nonconductors of electricity; shock absorbers; mountings for motors and other machinery; transmission belts; gaskets; hoses for transporting gases and liquids; transparent materials; translucent materials; articles of clothing to keep out rain or to control the figure; sports goods; cements; paints; plastics; pharmaceuticals; drug sundries; and, above all, tyres, the chief outlet for rubber (Polhamus, 1962, p. 14).

Indeed, rubber has become a ubiquitous feature in the daily work and leisure activities of virtually everyone in the industrialized world.

In the United States, the world's greatest producer and consumer of synthetic rubbers, much confusion prevails about the true value and uses of natural sources of rubber. Americans commonly believe that use of natural rubber is a phenomenon of the past, while nothing could be further from the truth. The two major reasons for this are that natural rubber, the most versatile of all rubbers, is still indispensible for many of its most critical uses; and that as a result of the present energy crisis and consequent increased prices for petroleum-based synthetics, natural rubber now faces a much brighter economic future than it has at any time during the past few decades.

In the first place, synthetic polyisoprene, a type of synthetic rubber, is our closest replica of the natural rubber molecule. It is modeled after the *cis*-1, 4-polyisoprene hevea molecule which cannot be easily duplicated synthetically. It has a molecular weight greater than 1 million and a great degree of geometrical regularity. A unique toughness associated with the natural *cis*-1,4-polyisoprene molecule has

enabled it to retain its supremacy over synthetics for many of its most demanding uses. Prime examples come from the tire industry, the greatest user of natural rubber. Large tires, or those designed to function under low pressures, are prone to heat build-up from excessive flexing. Whereas synthetic rubber is very susceptible to destructive heat build-up, natural rubber exhibits less crack growth, lower hysteresis, and a greater capacity to adapt to temperature changes. Its performance under high temperatures is thus superior to that of the synthetics. As a result, heavy-duty tires, such as those used for trucks, buses, and off-road vehicles for farm, construction, or other rugged industrial purposes, typically contain a greater proportion of natural rubber. The plant-derived product still comprises 90-100 percent of the rubber in airplane tires, and the best-performing radial tires are composed of a greater percentage of natural rubber than is commonly employed in the manufacture of most passenger car and truck tires. In comparison with nonradial tires, in the United States, steel-belted radial passenger tires require about 100 percent, and radial truck tires, 160 percent, more natural rubber. The proportion of natural to synthetic rubbers in these products is often lower when they are manufactured in the United States than in Japan or Europe. This difference has been largely due to the availability and lower cost (in the United States) of petroleum-based rubber as compared with natural rubber. However, this situation is expected to reverse in the near future since the actual and relative cost of petroleum is currently increasing and fossil fuels are becoming more scarce. Thus, the percentage of natural rubber in these products should increase accordingly.

In the United States, more than 70 percent of the natural rubber imports are used for the manufacture of tires. Other uses of natural rubber (1960) include: industrial products (10 percent); carpets (5 percent); foam and sponge products (4 percent); shoe products (2 percent); thread and rubber cements (2 percent); drugs and sundries (1 percent); and miscellaneous products (4 percent). Although synthetic rubber will continue to be an important component in most of these products, and it is actually preferred for the manufacture of certain items, it has not and cannot totally replace the need for natural sources of rubber. The demand for natural rubber will increase as the demand for tires and other heat-resistant rubber products increases.

The second major reason that natural rubber will remain an important commodity in international trade is that it has recently attained a better cost-competitive position relative to the petroleum-based synthetics. Natural rubber supplied 100 percent of the world rubber needs prior to World War II. However, synthetic rubber, developed in the United States during the war, quickly became established as a rubber substitute at that time. It removed the necessity of expensive, lengthy shipments of natural rubber, and was more easily suited to industrial application by virtue of its greater chemical uniformity. During the "rubber boom" that followed World War II, the widespread adoption of synthetic polyisoprene rubber, particularly in the United States, led many economists to predict an early decline of natural rubber in world markets. Indeed, its relative importance worldwide has declined, from its exclusive use up to the 1940's, to around 33 percent in 1976. Yet in spite of the prediction of an early decline, natural rubber production has, in fact, tripled, since the last world war, and today, more than 3.8 million metric tons are used annually. Moreover, the future for natural rubber now looks better than ever. Recent demands presently exceed the total supply, and some projections indicate that by 1980, about

40 percent of world demand may be met by plant-derived elastomers (provided production goals can be met). As early as 1964, an industrial periodical observed that the five largest American rubber-producing firms, that "have been hard-selling synthetics," were expanding their investment and interests in natural rubber. Why has this course of events occurred?

Many economically related factors have contributed to this situation. One is an increased demand for products that utilize a higher proportion of the natural product. As an example, recent industry and consumer trends indicate that radial tires are being increasingly favored over ordinary passenger car or truck tires which require approximately half or less of the natural rubber content of radials. Whereas only 3 percent of the 1970 automobile tire market was supplied by radial tires, by 1980 radials are projected to supply more than half the entire market. The radial truck tire market in the United States, less than 3 percent in 1970, should reach almost 30 percent by 1980, and in Europe, over 80 percent, up from 58 percent.

The other important reasons are related to the dramatic shift now taking place in the relative cost of producing synthetic versus natural rubber. First, it appears that cost increases in the production of synthetics currently vary directly with wage rate increases in the developed nations which produce the bulk of synthetic rubber. In contrast, natural rubber is produced in the less technologically advanced countries which generally have lower wage rates. Second, rubber-bearing plants, including both hevea and guayule (*Parthenium argentatum*), are suitable for cultivation on lands ill-suited for production of agricultural produce. Third, the production of synthetic rubber is a far more energy-intensive process, and it requires the use of petroleum-based or nonrenewable energy materials that are rapidly rising in cost. Alternatively, hevea and other plant sources of crude rubber, such as guayule, are renewable resources produced by the free energy of the sun and are not currently in demand for competing economic uses. Moreover, as biologically renewable resources, these plant species can be genetically improved for higher rubber productivity, a strategy that cannot be applied to petroleum reserves. The development and extensive use of genetically improved strains or clones of rubber-producing plant species can significantly increase rubber yields and reduce the costs of natural rubber production. Last, new chemical and biologically based techniques in the production, extraction, and processing of natural rubber have opened new avenues for the exploitation of this natural, plant-derived industrial material. Recent developments, such as "chemical bioinduction" for increasing plant yields of extractive raw materials, are actually enhancing our possibilities to "mine" oil or hydrocarbons from rubber- and oil-bearing plants.

Domestication and Genetic Improvement of the Pará Rubber Tree

The Pará rubber tree, *Hevea brasiliensis* (family Euphorbiaceae) (Fig. 1), is for all practical purposes the world's sole source of natural rubber. However, in the early years of rubber production, no one species was favored as a sole or primary source of this important industrial raw material. The history of natural rubber production from this particular species provides an interesting and illustrative story about mankind's exploitation of the genetic resources available within natural environments.

Fig. 1. The Pará or hevea rubber tree *(Hevea brasiliensis).* (Photo: The Malaysian Rubber Bureau)

Prior to 1900, natural rubber was extracted from wild populations or cultivated plantings of many different genera and species including maniçoba rubber (*Manihot glaziovii*, family Euphorbiaceae) (Fig. 2), Panama rubber (*Castilla elastica*, family Moraceae) in tropical America, the India rubber-fig (*Ficus elastica*, family Moraceae) in India, and landolphia (*Landolphia* spp., family Apocynaceae) in Africa. The eventual choice of *Hevea* over other rubber-producing taxa and our present, almost exclusive, reliance on this species today is the result of a number of

Fig. 2. A cultivated stand of Ceara rubber or Ceara manicoba *(Manihot glaziovii).* A euphorb species of northeastern Brazil, this small tree was used as a source of rubber during the early 1900's and World War II. It can be tapped repeatedly and produces a good quality rubber, but its productivity is very low and uncertain in comparison to that of its distant relative, *Hevea brasiliensis.* (Photo: U.S. Forest Service, USDA)

biologically related factors. First, about 90 percent of the composition of hevea crude rubber is high-quality polyisoprene; in constrast, other rubber-producers typically yield a much lower proportion of polyisoprene relative to their nonrubber constituents. Second, compared with high-yielding *Hevea* species, many other species do not yield sufficient quantities of crude rubber. Last and most important of

Fig. 3. Unlike the rubber-producing euphorbs, *Castilla* or Panama rubber trees cannot withstand repeated tappings; once the latex vessels are severed, the canals will usually continue to drain until nearly all of the latex has been released. Panama rubber trees therefore often die after tapping, or they may require several months to recuperate before a second tapping. For this reason, they are usually tapped only once, and they are often felled afterwards. Prior to the arrival of Europeans in the Americas, native Amerindians probably used *Castilla* more than any other rubber-bearing species. Panama rubber was of greater commercial importance than hevea rubber until the mid-nineteenth century; by that time, overexploitation of wild *Castilla* stands and the success of the *Hevea* rubber plantations of the Far East brought about its decline as a commercial species. (Photo: National Archives)

all, unlike many other rubber-bearing plants, *Hevea* is highly adaptable to cultivation, especially since it withstands repeated tappings; latex yields actually increase with repeated tappings, and no production advantages can be obtained by felling hevea trees. Overall yields are lower from taxa that must be "sacrificed" or killed for maximum production of latex, such as the *Castilla* species of tropical America (Fig. 3) or those of the genus *Landolphia* in Africa. Moreover, wild stands of rubber-producing species that had to be cut or were felled became quickly depleted from overexploitation whenever the demand for rubber was great. Thus *Castilla* and *Landolphia* populations were overharvested during the early days of rubber production. Furthermore, during the rubber booms of the early 1900's and World War II, both guayule (*Parthenium argentatum*, family Compositae) in Mexico and mangabeira (*Hancornia speciosa*, family Apocynaceae) in tropical America were similarly depleted. The depletion of *Castilla* in the Amazon Basin was a primary motivation for the switch to *Hevea*.

When the demand for natural rubber soared after the discovery of the vulcanization process in 1839, the need for adequate, continuous supplies of this new industrial material provided a further impetus to establish rubber-producing plantations. Thus, in 1870 the same official who was responsible for the collection of germplasm from the disappearing quinine-bearing plant, *Cinchona*, suggested the procurement of genetic resources of a suitable tropical rubber-producing plant for an Asian-based industry. However, the eventual success of the Old World hevea plantations was in part due to two fortunate events which occurred during the initial collection and transport of hevea germplasm resources from the Amazonian rain forests of Brazil. The first stroke of luck was the selection of *H. brasiliensis*, a good producer of high quality latex; it is now known to be superior to seven other *Hevea* species and their numerous hybrids that yield inferior rubber. About 70,000 short-lived seeds of this particular species were collected from a site along the Tapajoz river by Henry Wickham in 1876. Wickham, who was not a botanist, relied upon the knowledge of Amazonian natives for the collection of the hevea germplasm. By chance, his party happened to gather seeds from an area where only *H. brasiliensis* was available. Had he collected elsewhere, he would likely have selected germplasm from more common, but inferior genetic resources, especially since *H. brasiliensis* has a very restricted distribution in the Amazon Valley. If this had occurred, the domestication and cultivation of *Hevea* would likely have been delayed by many decades everywhere.

The second lucky accident was that Wickham's seed stock was not infected with the fungus *Microcyclus* (= *Dothidella*) *ulei,* or South American leaf blight (SALB). This disease organism is the major factor limiting the culture of *Hevea* in the American tropics, and the history of rubber production would certainly have been very different if SALB had been introduced along with Wickham's original material. If this had occurred, it is possible that an alternative rubber-producing species might have been domesticated first, or the New World hevea industry might have succeeded instead because of its greater access to SALB-resistant, wild hevea genetic resources in the Amazon region.

Of the 70,000 SALB-free, high-yielding *H. brasiliensis* seeds transported from the Amazonian rain forests to the Royal Botanic Gardens in Kew (England), only 2,397 survived to make the final journey to the Orient. However, the Old World hevea plantation got a solid start in 1876 with these few seedlings from Wickham's

disease-free *H. brasiliensis* stock. Twenty years later, after many seed multiplications and the development of the practical Ridley method of tapping hevea, rubber producers in the Far East established the first commercial plantings in the late 1890's. By the 20th century, the rubber industry suddenly assumed expanded importance when an increase in consumer demand for the newly developed automobile enhanced the demand for rubber tires. Although the first seedlings derived from Wickham's unselected wild plants yielded a mere 2.0 kg (4.3 lb) of dry rubber per tree each year, the more dense, cultivated stands of *H. brasiliensis* slowly began to outcompete other cultivated and wild sources of natural rubber. By 1912 the production of cultivated hevea rubber equalled that of latex produced from all other sources, and efforts to genetically improve the yields of the Wickham stock were already underway. Thus, by the beginning of World War II, production from wild African and Amazonian plants was economically insignificant.

Today essentially the entire natural rubber industry is still founded upon the descendants of Wickham's sample of wild *Hevea brasiliensis.* The economic success of the Old World plantation rubber industry can be attributed to two major factors involving the location and manipulation of hevea genetic resources. One of these was the ability of the Asian rubber-producers to increase the yield and rubber quality of the original Wickham stock. At first, this was achieved via cultural methods, e.g., the new methods of tapping improved long-term yields and reduced rubber impurities. Later, however, selection and crossbreeding within the Wickham stock led to astonishing yield increases. The native Brazilian pollinators of the hevea trees from which Wickham collected his seeds are today believed to have played an important role in developing the genetic lines used as parent material for breeding the high-yielding Asian genotypes. As with many tropical rain forest trees, *Hevea brasiliensis* plants are rare and widely scattered throughout their habitat, at densities of about one tree per hectare (two trees per acre). The main pollinators of hevea are tiny thrips and midges. Because these insects do not fly over great distances, such as those which separate many of the individual trees in the Tapajoz River population, most of Wickham's trees were probably largely self-pollinated or pollinated by a few close neighbors. Thus, his seed samples were likely derived from relatively pure inbred lines. For this reason, the progeny of later artificial cross-pollinations exhibited hybrid vigor (heterosis); and the unselected seedlings from these crosses demonstrated great variability in yield. About 10 percent of the offspring from these matings possessed the potential to yield 3-6 times more latex than either of their inbred Tapajoz parents.

The Asian plant breeders selected among the progeny derived from these early crosses, genetically fixed the highest yielding genotypes by obtaining clones via bud-grafting, and then used them for parental stock in subsequent crosses. Repetition of this process over many generations led to the development of a number of high-yielding hevea clones. Thus, although the unselected trees first collected by Wickham produced only about 225 kg/ha (200 lb/acre) of rubber annually, even using the best tapping methods available at that time, by the 1930's average Malaysian plantation yields were higher than 400 kg/ha (360 lb/acre). Production in some experimental plots established by the Rubber Research Institute of Malaysia of clonal RRIM rubber neared 1,000 kg/ha (890 lb/ac) in the 1930's; the best of these genotypes were planted commercially in the 1950's. More recent improvements developed during the war have raised average plantation yields to 1,200-1,600 kg/ha (1,070-1,425 lb/acre)

in recent years. Furthermore, yields on the 1970's experimental plots with RRIM 703 are 130 percent higher than the yields possible with the best RRIM 500 series clones of the 1950's. Some of these recent experimental plots produce 2,500-4,040 kg/ha (2,230-3,600 lb/acre) of crude rubber annually; and new planting materials derived from these genetically improved stocks can yield up to 3,000 kg/ha (2,680 lb/ac). Indeed, few other crops can equal this 100-year record of a more than tenfold increase in yield.

The second and most important factor contributing to the success of the Old World plantation industry has been its ability to operate in the absence of SALB. As noted previously, probably the most important general rule for enhancing crop productivity is introduction of economically valuable plants to suitable alien environments without the concomitant introduction of their native pests and diseases. The successful transport of hevea to Asia without its major native disease, SALB, is a case in point. Although once narrowly restricted to the natural range of hevea species within the Amazonian region, this fungus has spread throughout the Americas wherever the cultivation of rubber has expanded. Each time a new, "clean" plantation was established, or an unmaintained, overgrown plantation cleared of its secondary jungle growth, SALB easily attacked the more densely cultivated stocks in epidemic proportions.

Apparently, natural populations of wild hevea trees are so scattered that they are not seriously affected by the fungus. Plantation stocks that had been extensively invaded by weedy companion trees were also spared the ravages of SALB. Thus, removing the protective canopy of intervening rain forest vegetation associated with hevea renders crowded plantation trees especially vulnerable to epidemics caused by this pathogen. Almost "single-handedly," this organism has prohibited or retarded the establishment of hevea rubber plantations in the Western Hemisphere, such as those attempted by the the Ford Motor Company and the Goodyear Plantation Company during the 1920's and 1930's. Both companies attempted to utilize the improved, high-yielding clones previously developed in Asia; however, they found this breeding material extremely susceptible to SALB. Moreover, they quickly discovered that the immediately accessible Amazonian genetic resources either were low-yielding or, alternatively, were susceptible to the disease.

The only possible solution to the situation was the foundation of a viable breeding program to develop high-yielding, SALB-resistant hevea clones. This was finally initiated during the 1940's in the haste of an oncoming war. In December 1941, the United States' and its Allies' position was perilous when the Japanese occupied the Asian rubber-producing areas which at that time produced 90 percent of the world supply of rubber. Many people today fail to understand the urgency of this situation, or the importance that natural rubber played during both world wars. During the First World War, Germany was unable to secure or to produce an adequate supply of natural rubber, and this failure has been cited as one of the major reasons for that nation's defeat. By the Second World War, the United States was in a similar situation. Our earlier efforts to establish New World plantations had been fruitless, and by 1940 wild rubber production in Latin America was economically insignificant. Moreover, at that time, the supply of newly developed synthetic rubbers was inadequate for critical wartime needs, and basic research necessary to develop disease-resistant hevea clones for SALB-infested areas had still not been conducted. In short, the country was facing a modern war, technologically

dependent on an ample supply of a scarce, but strategically essential industrial raw material.

The rubber crisis of World War II resulted in the creation of the USDA Cooperative Rubber Research Program (CRRP), which attempted to enhance dwindling rubber supplies from wild sources. Rubber was extracted for the war effort from many wild plant sources, including *Hevea*, *Castilla*, *Manihot*, *Landolphia*, *Ficus*, and *Parthenium* (Fig. 4); and a concerted effort to develop high-yielding,

Fig. 4. Native laborers or "guayuleros" harvesting wild guayule *(Parthenium argentatum)* in Mexico during World War II. During the war, the USDA Cooperative Rubber Research Program procured supplies of natural rubber from a variety of wild, rubber-bearing plant species, including guayule. (Photo: National Archives)

SALB-resistant hevea strains was also initiated. An alarmed Congress provided the new program with a modest budget. Its scientists benefited from the information gleaned from the disastrous South American experiences of the Goodyear and Ford plantations with *Hevea*. Although the war ended long before the desired breeding results were accomplished, this tree improvement program made considerable progress toward the development of disease-resistant hevea clones. USDA scientists made surveys in the Amazon for prime genetic materials (Fig. 5), established central testing stations to evaluate them, and assembled collections of potentially useful hevea clones and seeds. By the time the project was terminated 14 years later, they had developed several hundred clones which demonstrated sufficient resistance to the two major native Amazonian leaf diseases; some of these strains possessed near-commercial yields. Besides this, they had developed three-part, grafted trees for more immediate or short-term uses. A feat of horticultural engineering, these three-component trees consisted of vegetative materials derived from three different *Hevea* genotypes: a crown or canopy clone resistant to SALB, a high-yielding trunk or

Fig. 5. U.S. scientists surveyed the Amazon basin during World War II in an effort to locate suitable wild stands of hevea trees for immediate tapping and "elite" germplasm resources for the development of high-yielding, SALB-resistant *H. brasiliensis* trees. (Photo: National Archives)

"panel" clone, and a root disease-resistant rootstock. One of the most important achievements of CRRP, however, was the delineation of important Amazonian genetic reservoirs that contain superior or potentially useful hevea gene pool resources.

Even though the USDA hevea research program never contributed materially to the war effort *per se*, the time and expense allotted to it was not spent in vain. Much of the breeding work has been continued by private corporations and rubber research institutions; pathology research is still conducted at all the national rubber research institutes, and the accomplishments of these combined programs will provide valuable genetic resources for future emergencies as well as more short-term economic needs. The major emphasis of most of these breeding programs is the incorporation of disease-resistance traits while retaining the high-yield characteristics of the best *H. brasiliensis* clones. Each country tends to be concerned with the diseases (pests) endemic to its own areas: Brazil leads the research against SALB; In-

dia and Thailand are studying *Phytophthora* leaf fall; and Malaysia and Sri Lanka are the leaders in *Oidium* and *Gloeosporium* leaf diseases and white root disease. Among the many diseases of the hevea rubber tree, SALB remains the most serious threat to the future of natural rubber production. In order to succeed, hevea culture in the Amazon Basin must eventually be based on planting materials with polygenic or multiple-gene resistance to the major strains of SALB. Moreover, for the plant breeders and business interests associated with this important industrial crop plant, one of the greatest fears is that hevea's worst enemy might reach the major rubber-producing region of the world in Southeast Asia. If SALB were accidentally or intentionally introduced to this area, the production of natural rubber would cease almost entirely, effecting the unemployment of millions. The rubber industries and governments of the major rubber-producing nations are fully aware of this possibility, and they are prepared to attempt eradication in the event that SALB appears in their area. However, at present, multiple-gene SALB-resistant hevea clones that produce commercial yields do not exist. Some blight-resistant clones were imported from Brazil to Sri Lanka during the 1950's for breeding purposes. More recently the Rubber Research Institute of Malaysia has incorporated a few South American clones in its breeding program, and the Brazilian government has cooperated in an expedition for germplasm collection. However, the germplasm base for selecting SALB-resistant genotypes remains small in Southeast Asia, and there is little time left to spare in developing and using a good backlog of clones, cultivars, and planting stocks with a broad base of resistance to SALB.

The wild hevea genetic resources scattered throughout the Amazonian rain forests play a central role in the search for resistance to SALB and other pathogens. Germplasm from wild populations of both *H. brasiliensis* and a number of related, commercially worthless species have been employed in disease-resistance breeding programs. For example, the development of SALB-resistant *H. brasiliensis* x *benthamiana* hybrids, initiated by the Ford Motor Company in the 1920's, has been continued by the Cocoa Research Institute (CEPEC) of Brazil. In general, *H. benthamiana* possesses good levels of resistance to SALB but produces only low to moderate yields of good quality latex. Nevertheless, some of the best *H. benthamiana* hybrids have been reported to yield up to 2,000 kg/ha (1,785 lb/acre) annually under commercial conditions (in the presence of SALB). An alternative program to combat SALB has also been initiated in Brazil. This program emphasizes the use of the highly resistant (perhaps totally resistant) species, *H. pauciflora*. In general, however, the yield and quality of the latex of this species is inferior to that of *H. benthamiana*. Yet high-yielding *H. brasiliensis* x *benthamiana* hybrids have been crossed with the more resistant *H. pauciflora*, and the progeny of these crosses are reported to possess twice the vigor of their high-yielding parents. The Firestone Company has enlisted an entirely different approach, using only the natural variability available within *H. brasiliensis*. Firestone has conducted 15 years of breeding with wild *H. brasiliensis* genetic resources from the Madre de Dios area in Peru. Trees from this area possess significant levels of SALB-resistance and higher than average yields. These were crossed with the susceptible but superior-yielding Asian stocks (RRIM clones), and the best of 2,500 seedlings were selected for further breeding. Today some blight-resistant genotypes suitable for commercial use have been identified.

Progress has also been made against other hevea pathogens. For example, a breeding program in Costa Rica has demonstrated that resistance to *Phytophthora*

leaf fall can be attained through plant breeding. Although *H. pauciflora* is highly resistant to *Phytophthora*, the most promising clones—those which showed a high degree of resistance—were derived from an otherwise commercially useless species, *H. rigidiflora*. Only one of the clones that survived a serious outbreak of *Phytophthora* in Costa Rica and possessed a notable degree of resistance was derived totally from *H. brasiliensis* parentage. Most of the surviving, resistant clones (six) were hybrids between this preferred economic species and *H. benthamiana*, and three more were clones of the latter species. Another was a natural hybrid between *H. brasiliensis* and *H. spruceana*, a species that yields inferior rubber; similar crosses between these two species have produced rootstock hybrids that have shown promise against a root disease in the Americas. Other species that produce an inferior quality or yield of latex, but that may one day be useful for the improvement of high-yielding *H. brasiliensis* clones are: the SALB-resistant and drought-tolerant *H. nitida*; the cold-adapted *H. guianensis*; an endemic, water-tolerant species, *H. microphylla*; and a dwarf species, *H. camporum*.

Already, substantial economic benefits have accrued from the genetic improvement of the Pará rubber tree. As Loren Polhamus (1962), one of the organizers of the USDA Cooperative Rubber Research Program, has observed:

> Plant improvement through the development of high-yielding clones has been the most successful method of increasing rubber yields and reducing costs on the Eastern rubber plantations. Thus research has paid off in increased supplies of rubber, and may be expected to contribute materially to further increases (p. 197).

The importance of preserving the hevea genetic resources of the Amazon regions of South America for future breeding cannot be overemphasized. At present, conservation of hevea germplasm in its native habitat is the most adequate and appropriate means of ensuring success in the breeding programs of the future. Hevea seeds, like the seeds of many other tropical timber and fruit trees, cannot be dried or frozen without injury and loss of viability; such recalcitrant seeds cannot be stored effectively by cold storage *ex situ* methods. And as yet, no one has reported the regeneration of an entire hevea tree from hevea cells via tissue or cell culture techniques. Even if this technique had been perfected for hevea, there are still problems in maintaining plant tissues and individual cells in a genetically stable state. Moreover, the prospects for supplanting natural sources of variation with artificially induced mutants or polyploids has not yet produced promising results.

All of these difficulties point to the value of conserving wild hevea populations in their native Amazonian rain forest habitats. Hevea reserves would include a wide array of other economically important tropical biota as well. The Amazon region is currently undergoing rapid economic development. Many parts of the rain forest are being cut or otherwise destroyed, and transformed into monocultural tree plantations, indigenous agro-ecosystems, grazing areas, highways, or human settlements. In 1976 the International Board for Plant Genetic Resources ranked the gene center in Brazil which contains hevea as a second priority area—one in critical need of collection and conservation of hevea germplasm resources. At least eight of the fifteen major development areas in Brazil's new Polamazônia project overlap with a significant portion of the natural distribution of *Hevea brasiliensis per se*, and three other developments overlap significantly with the distribution of other *Hevea* species. As much as 20 percent of the natural habitat of *H. brasiliensis* may be currently slated for development. Given the urgency of this situation, and the large expanses of its

natural habitat that will disappear in the near future, both conservation of *Hevea* populations in the Amazon Basin and elsewhere should be a paramount concern. The future of the Pará rubber tree as one of the world's most important industrial crop plants ultimately may depend on the effectiveness of present conservation efforts.

Guayule and Other American Sources of Natural Rubber*

In spite of the current economic importance of hevea rubber to our economy, many other rubber-producing plant species merit consideration as alternative sources of natural rubber. Since *Hevea brasiliensis* has been greatly improved after only a few decades of intensive selection and breeding, other perennial rubber-bearing species might be similarly developed within a relatively short period of time. The United States relied upon one of these, guayule (*Parthenium argentatum*), as an emergency source of rubber during World War II. Today renewed interest in this native American plant centers on its use as an elastomer substitute for either hevea rubber or costly petroleum-based synthetics. Furthermore, considering restrictions on the availability of imported hevea rubber, the United States may one day need to use guayule in the event of another national emergency. As an alternative strategy, the United States could domesticate and utilize any number of other rubber-bearing species that are better adapted to more temperate climates, even though attention would have to be paid to the development of disease- and pest-resistant strains.

Approximately 2,000 plant species are known to contain the valuable *cis*-1,4-polyisoprene type of rubber, and a number of these are temperate or subtropical species. Some of the most important promising U.S. rubber-bearing species are listed in Table 1. One of these species, the common milkweed (*Asclepias syriaca*), is illustrated in Fig. 6. Most of these rubber-producing species are members of plant families Apocynaceae, Asclepiadaceae, Compositae, Euphorbiaceae and Moraceae, those that typically contain many taxa that produce a milky sap or latex. However, only a small number of these species produce sufficient quantities of rubber to justify commercial extraction. Of the latex-producing species used commercially in the past, none is native to the United States except guayule. The chemical structure and molecular weight of guayule rubber is very similar to that of hevea rubber. Moreover, vulcanized guayule rubber, when supplemented with additional fatty acids, possesses comparable curing rates and very similar physical properties to vulcanized hevea rubber. Thus, it appears that guayule rubber of a "technically specified" type can be employed as a direct economic substitute for hevea rubber. Furthermore, both types of natural polyisoprene rubbers possess chemical and physical properties superior to those of synthetic polyisoprenes.

The guayule plant is a perennial desert shrub which thrives in the subtropical-temperate climates of the upland plateaus of Mexico and Texas (as opposed to hevea cultivation which can be undertaken only in restricted areas of the humid or wet tropics). It requires less annual rainfall than most irrigated crops in the desert Southwest, and may be grown in many semi-arid areas where water supplies are er-

*Pronounced "wy-oo-lee."

TABLE 1. Some U.S. Plants Currently Under Investigation As Sources of Natural Rubber

Latin Name	Common Name	% Natural Rubber	Ave. Molecular Weight
Asclepiadaceae	Milkweed family		
Asclepias incarnata	Swamp milkweed	1.69	—
Asclepias subulata	Desert milkweed	2.95	—
Asclepias syriaca	Common milkweed	1.39	120
Caprifoliaceae	Honeysuckle family		
Lonicera tatarica	Red tarterion honeysuckle	1.64	298
Compositae/Asteraceae	Sunflower family		
Cacalia atriplicifolia	Pale Indian plantain	3.10	265
Chrysothamnus nauseosus	Rabbitbrush	1.67	—
Parthenium argentatum	Guayule—young plant	4.58	1280
	Guayule—adult plant	20.00	1280
Solidago graminifolia	Grass-leaved goldenrod	1.43	231
Solidago leavenworthii	Edison's goldenrod	1.37	118
Solidago rigida	Stiff goldenrod	1.39	164
Labiatae/Lamiaceae	Mint family		
Pycnanthemum incanum	Western mountain mint	1.24	495
Teucrium canadense	American germander	1.32	130

Sources: Buchanan and Otey, 1978; Buchanan et al., 1978.

Fig. 6. The common milkweed *(Asclepias syriaca)*. Approximately 1.5 percent of the chemical composition of a common milkweed plant is low molecular weight natural rubber. With genetic improvement for greater yield of higher molecular weight hydrocarbons, this perennial species could become an important U.S. rubber-producing species. (Photo: USDA)

ratic or unreliable. Presently, 30 percent of the surface of the earth is desert, and this percentage increases yearly in many areas of the world as a result of overgrazing and other forms of vegetation removal. Clearly, arid-adapted plants such as guayule comprise unique genetic resources for enhancing the economic potential of semi-arid or arid environments.

Guayule rubber was first displayed to the United States in an exhibit from the state of Durango, Mexico at the 1876 Centennial Exhibition in Philadelphia, and the first commercial extraction of guayule rubber in the United States occurred in 1888. However, extensive American experimentation with *Parthenium argentatum* as a source of crude rubber began shortly after the turn of the century. The bicycle craze of the 1890's was followed by an automobile craze, and rubber was in great demand for tires. The invention in 1902 of the "pebble mill" method for extracting guayule brought many mills or factories to Texas guayule country. The customary practice was to build a factory within the central part of a large concentration of wild guayule shrubs. Then "baling camps" were dispatched to various parts of the "range"; there the guayule was harvested, baled, and packed by burro to the mill for processing.

By 1905 the Mexican mills were annually producing 341,000 kg (750,000 lb) of crude guayule rubber. In 1909 the United States imported 9,390 metric tons (9,540 long tons) of guayule rubber from Mexico, almost twice as much as its hevea rubber imports. In the following year, the production of the Mexican mills reached 9.5 million kg (21 million lb). Each year most of Mexico's guayule rubber was exported to the United States, and guayule's value as a source of rubber soon attracted the attention of some of the leading U.S. industrialists, notably John D. Rockefeller, Daniel Guggenheim, and Francesco Madero. By 1911 these and other prominent American industrialists reputedly had invested more than $30 million in the development of the wild Mexican guayule industry. By that time the import demand had become great enough to encourage the establishment of a guayule extraction and processing company at Marathon, Texas, in the heart of the Big Bend country.

Thus, by the end of the first decade of the 20th century, the extraction of rubber from wild guayule stands had already become a very profitable and thriving economic venture. In addition to the U.S. mill at Marathon, as many as 13 Mexican mills were operating at one time. However, since harvesting required the sacrifice of individual plants, the economic progress of the industry was being made at the expense of the wild guayule stands. Early estimates of resource availability had predicted that, under the pressure of such heavy and sustained economic exploitation, the wild sources of guayule would be exhausted in about 17 years. By 1910 these predictions appeared to be accurate, since many of the once vast Mexican stands were showing signs of depletion and some stands had been completely denuded of all the guayule that was worth harvesting. Lack of raw material caused factory after factory to close, until the major producing firm of that time, the Mexican Continental Rubber Company, was practically the only remaining producer. Concerned about the potential exhaustion of their remaining resource base, the company began to protect their future supplies of guayule by permitting the harvest of only mature shrubs. More important, however, the company acted, with considerable foresight, to encourage the cultivation of guayule. In 1910, the firm hired Dr. W. B. McCallum to solve the difficulties of guayule seed germination. Until that time, cultivation efforts had failed because it was difficult to induce germination of the seeds.

After discovering a method for seed germination, McCallum initiated what was to become a lifetime of work on the selection and genetic improvement of *Parthenium argentatum*. His work in this direction began at Torreon, Mexico; however, he relocated to California with the new industry in 1912 when the Mexican revolution broke out. There the firm became known as the U.S. Intercontinental Rubber Company. McCallum quickly discovered that some of his wild guayule strains were highly productive, whereas others were essentially worthless as rubber producers. Until the 1920's he conducted cultural experiments with selected genetic strains of guayule in California and Arizona. In 1925 some of the better strains were planted on 3,239 ha (8,000 acres) in the Salinas valley of California. The best of these genotypes were yielding over 100 percent more than the average rubber yields derived from unselected wild shrubs. Shortly after the establishment of these highly productive strains, however, two unfortunate events led to the demise of this infant industrial project. In the early 1930's, irrigation spread rapidly, making alternative types of agriculture feasible. Concurrently, rubber prices slumped in the mid-1930's during the Depression. As a result, many of the guayule fields were plowed under or burned. Yet in the decade between 1931 and 1941, more than 1.4 million kg (3 million lb) of crude guayule rubber had been processed at the Salinas mill, averaging 785 kg/ha (700 lb/acre).

In spite of the economic setbacks it had suffered, this early American rubber project had already received notable recognition. The U.S. War Department, concerned about the low U.S. stockpiles of rubber and the military vulnerability of the Asian rubber-producing region, sent two men to visit the Salinas valley in 1930. In their report of June 6, 1930, Majors Dwight D. Eisenhower and Gilbert van B. Wilkes reported quite favorably on the prospects of guayule as a U.S. industrial crop:

> We are personally convinced that under real encouragement the production of guayule would develop rapidly into an important industry in the United States (Taylor, 1951, p. 259).

Moreover, they advised that guayule should have been established already as a farm crop on the arid, marginal lands of the United States, in order to augment the nation's domestic supplies of natural rubber in the event of a "grave emergency." Nevertheless, their warnings and suggestions passed largely unheeded by Congress.

The U.S. government showed no further interest in guayule—that is, until it entered World War II after the bombing of Pearl Harbor in December 1941 (Fig. 7). The United States had come to rely heavily on supplies of hevea rubber by that time, and as late as summer 1941, a bill to initiate emergency plantings of guayule was voted down. Thus, the Japanese occupation of the hevea rubber-producing region in Southeast Asia early in 1942 precipitated a rubber crisis for the Allied Forces. Rubber tires and other rubber products were essential components of the war machinery *per se*, as well as the equipment needed for transporting troops and distributing critical war supplies. Even though the United States had synthesized more than 8,000 tons of rubber by 1941, synthetic rubber was still more of a curiosity than a reality at that time.

The lack of hevea rubber supplies from Indonesia and Malaya placed the United States and its Allies in a critical position. Exploitation and development of all available rubber-bearing plant species that yielded sufficient quantities of suitable-

Fig. 7. Machine cultivating guayule shrubs *(Parthenium argentatum)* in Salinas, California in December 1941. At the outbreak of World War II, the United States was fortunate to have a domestic supply of cultivated rubber plants in California at the U.S. Intercontinental Rubber Company. The founder of this company, Dr. W.B. McCallum, had already devoted three decades to the selection and genetic improvement of stocks of wild Mexican guayule. The 2-year-old plants in this field were derived from the best of McCallum's high-yielding genetic strains. (Photo: National Archives)

quality rubber were greatly needed. Ten days after the bombing of Pearl Harbor, a new bill was introduced to institute The Emergency Rubber Project (ERP) to fill this need. The bill authorized the negotiation and purchase of the holdings of the U.S. Intercontinental Rubber Company, including their seeds of guayule strains which McCallum had improved through selection. On March 5, 1942, Congress finally passed the bill, and President Roosevelt signed it on the same day. The U.S. Forest Service, which had been chosen as the action agency for growing the guayule, planted 39,000 seedlings to celebrate the occasion. Experimental plantings of other wild species were also initiated, particularly palay rubber (*Cryptostegia* spp., family Asclepiadaceae) which was transported from Madagascar to Haiti, and the Russian dandelion (*Taraxacum kok-saghyz*, family Compositae) from Russia to the United States (Fig. 8). However, the greatest focus of the ERP was guayule.

The enacting legislation authorized the planting of 30,350 ha (75,000 acres) of guayule initially, and later Congress increased the proposed area of cultivation to 202,350 ha (500,000 acres). However, this goal was never realized. On November 30, 1945, little more than 3 years later, an order was issued for liquidation of the project. Harvests had been made from only 2,450 ha (6,048 acres) of guayule plantations (Fig. 9) and 1,030 ha (2,540 acres) of wild Texas shrubs. Almost 1.4 million kg (3 million lb) of rubber had been produced, a portion of which was utilized for sealing

Fig. 8. An experimental planting of 2-month-old Russian dandelions *(Taraxacum kok-saghyz)* at the Cass Lake nursery in the Chippewa National Forest, Minnesota in July 1942. Even though the primary focus of the Emergency Rubber Project was guayule, this project also initiated experimental work with other important rubber-bearing plant species that were preadapted for cultivation in American climates. (Photo: National Archives)

Fig. 9. At the time of the Second World War, cultivated stands of guayule shrubs were already being harvested by mechanical means. The machine harvester shown here is picking up the guayule shrubs, and chopping and loading them onto a truck bed. (Photo: National Archives)

fuel cells for military torpedo boats and aircraft. However, the December 1946 liquidation operation resulted in the destruction of two processing mills and other buildings, as well as 9.5 million kg (21 million lb) of unprocessed rubber from 10,930 ha (27,000 acres) of guayule. Thus, about 85 percent of the shrubs cultivated specifically for the war effort remained unharvested. Following the war, the interest in natural sources of rubber waned. Synthetic rubber, which had been developed and employed in the United States during the last years of the war, became widely available to consumers at that time.

Petroleum, the principal source of synthetic rubber, remained a relatively cheap industrial raw material throughout the 1950's and 1960's. Thus over the last few decades, the proportion of the total rubber market shared by the synthetic products steadily increased. By 1970, synthetics supplied more than 77 percent of U.S. rubber. Yet today, the trend is reversing, and the current prospects for natural sources of rubber are quite promising. During the next decade the demand for natural rubber is expected to increase by 5.9 percent each year, whereas the global supply of hevea rubber is likely to rise by only 3.8 percent annually. Moreover, natural rubber is still necessary for certain critical uses, and petroleum supplies for the production of synthetics are dwindling. The price of delivered crude oil (per barrel) has been steadily climbing, from only $3 in 1972 to around $12 in 1977 to $22 in 1979. And the price of styrene, butadiene, and other synthetic rubbers has increased accordingly. A 1977 National Academy of Sciences report on guayule stated that:

> In the long run, as the nation's petroleum disappears, guayule's greatest value may be as an alternative to the synthetic polyisoprene rubbers that are produced from petroleum. The guayule plant could become a renewable domestic source of polyisoprene rubber for the nation (p. 8).

The economic future of natural rubber is now looking so bright that Congress recently prepared to invest $30 million in the further development and use of guayule.

Nevertheless, the eventual success of guayule as an important industrial crop will probably depend on future breeding and cultural advances. Some researchers indicate that the yield of McCallum's best strain, No. 593, could be doubled or even quadrupled through further selection and hybridization. McCallum had selected strain No. 593 prior to World War II, and it was the most extensively planted strain during the war. The rubber yields obtained from it are far superior to those of unselected wild shrubs. As early as 1951, Taylor suggested that more than 200,000 tons of rubber could be produced from this strain on 1.2 million ha (3 million acres) of marginal, arid, or semi-arid farmland in Texas, Arizona, New Mexico, and California.

Currently, yield improvement research is being conducted in California and Arizona using a number of different strategies. One of these is interspecific hybridization between guayule and its wild, tree-like relatives, especially *P. tomentosum* var. *stramonium* (Fig. 10). Some of the hybrids that have been obtained from such crosses are 7 times the normal size of guayule plants. Other strategies include selection for greater amounts of rubber-producing tissues and higher ratios of bark to wood, and highly branched or vigorous, fast-growing shrubs. Studies of the relationship between chromosome numbers, rubber content, and guayule morphology may aid in the yield improvement process. Moreover, rubber production may be enhanced in guayule and other rubber-bearing plant species through the use of cer-

Fig. 10. Five-year-old plantings of guayule (left) and its tree-like wild relative, *Parthenium tomentosum* var. *stramonium* (right). The guayule plant is only 1 m (3 ft) high, while its wild relative is 4 m (13 ft) tall. These two species cross readily and produce fertile offspring; researchers hope to obtain large, fast-growing hybrid guayule plants which can yield good quantities of high-quality rubber. (Photo: Agricultural Research Service, USDA)

tain chemicals. This cultural technique, called chemical bioinduction, is a form of genetic regulation based on the operon theory of the "depression" of gene activity to stimulate the activities of certain enzymes (gene products), in this case, those that control the process of rubber formation in plants.

Other traits that appear to be under some degree of genetic control in guayule include: cold and drought tolerance, resin content, rate and size of growth, disease resistance, weed competition capabilities, and ease of defoliation for processing and harvesting. Some of these desirable traits are receiving high priority in a new guayule

breeding program in Arizona. This program, initiated in 1976, is focusing on the development of guayule strains resistant to charcoal rot, *Phytophthora* root rot, and *Verticillium* fungi. Moreover, an effort is also planned to develop cold-tolerant genotypes so that the present range of cultivation of this rubber plant might be extended. The primary breeding aim in this case is hybridization between guayule and the common mariola (*P. incanum*) which thrives at 2,440-2,740 m (8,000-9,000 ft) elevations throughout the arid southwestern United States.

In addition, guayule possesses a bimodal reproductive system unique in comparison to our major crop plants. By proper manipulations during cross-breeding or hybridization, hybrids are produced which can be induced to set fertile seeds without sexual fertilization. This means that most successful new hybrids or genetic combinations can be quickly and more easily genetically "fixed" to breed true in subsequent generations—a plant breeder's dream. Considering all of the breeding potentials for guayule, as well as the remaining wild stands in Texas and Mexico which can provide fresh sources of germplasm, it is not unusual for plant breeders to speculate that its productivity could be much improved over 1942 wartime yields. Moreover, given the successful history of hevea improvement, which has entailed slower breeding advancement due to its longevity and great size at maturity, substantial yield improvements for guayule seem more easily obtainable.

Unfortunately, however, in contrast to the amount of time and effort already expended on the genetic improvement of hevea, the selection and breeding of guayule has been sporadic and not as well funded. Furthermore, many potentially valuable breeding stocks were burned or destroyed following World War II, rather than maintained for future use. In addition, the severe depletion or elimination of many of the wild Mexican stands, particularly germplasm from the naturally high-yielding Durango (Mexico) populations, has probably resulted in the irretrievable loss of "elite" or especially valuable genetic resources. In spite of these drawbacks, much useful genetic variation still exists within this species and its other wild relatives, and a substantial portion of the Texas stands of guayule are already conserved *in situ* in Big Bend National Park. This protected area was recently designated as a biosphere reserve by the UNESCO Man and the Biosphere program. The populations within the park area may possess valuable germplasm resources which can be tapped for cold tolerance or other economically useful traits. Thus conserved by formal national protection and international recognition of the Big Bend National Park, this sizeable stand of guayule gene pool resources will now be available for the benefit of present as well as future generations of Americans as well as all the peoples of the world.

7

Natural Sources of Industrial Oils and Waxes

Many plant species, and a few animal species, can provide oils and other hydrocarbon compounds which can be extracted, processed, and refined for use as fuel oils, lubricants, chemical feedstocks, or other industrial raw materials. As the cost of petrochemicals continues to rise, production of these ''botanochemicals'' and animal-derived chemicals will become more cost-competitive. In fact some methods for converting biomass to fuel, such as direct combustion of wood and wood wastes by some industries, are already considered economically efficient as a means of energy production. Moreover, a few hydrocarbon products derived from plants or animals, for example, sperm whale oil and its recently discovered economic substitute, jojoba oil, are essential industrial raw materials which cannot be easily duplicated by petrochemical substitutes.

Although most people living in industrialized nations tend to believe that our current sources of energy are unrelated to the biotic environment, this is actually not the case. In the first place, the bulk of hydrocarbons we use today as fuel oils were actually synthesized by living organisms. In 1974, 97 percent of the energy consumed in the United States was derived from fossil fuels— petroleum, coal, and natural gas. The precursors of the hydrocarbons which now represent these important energy resources were produced by plants (and animals) millions of years ago. Moreover, plant tissues can be used today for production of any present-day fossil fuel. Secondly, in 1974 combustion of wood wastes equaled the energy contribution of all hydroelectric dams in the United States; and more of our national energy requirements were supplied by direct combustion of fuelwood and wood wastes (1.5 percent) than by nuclear power (1.0 percent). In comparison to nuclear power which generates large quantities of deadly radioactive wastes, production and use of natural hydrocarbons is very safe. We have yet to discover a safe, economical means of disposing of nuclear waste that will eliminate its long-lasting threat to human life

and our living environment. Much more time and effort will be required to develop relatively nonpolluting energy systems such as solar and wind energy, or those based upon the actual energy-capturing mechanisms of photosynthesis in green plants. However, until then, direct and indirect use of plant hydrocarbons will remain one of our safest and most readily available means of producing energy as our finite stores of nonrenewable fossil fuels continue to be exhausted.

Certainly, energy is needed to "turn the wheels of industry." However, industrial lubricants which reduce friction and wear of high-pressure, high-friction machinery are also indispensible to modern industry. Sperm whale oil and jojoba oil are unique industrial lubricating oils. In contrast to the animal lard oils, base mineral oils, and petroleum substitutes that have been employed as industrial lubricants, sperm oil, and its new substitute, jojoba oil, are not actually oils *per se*, but rather liquid wax-esters. The possibility of displacement of these unique natural products by synthetics is remote, since the chemical structure of these liquid waxes cannot be easily synthesized commercially and they are superior for many of their most important industrial applications.

Hydrocarbons and Fuel Oils from Plants

Biomass conversion, the conversion of plant and animal organic matter into fuel oils, hydrocarbons, or other sources of energy, is a viable renewable resource option for meeting a portion of our global and national energy needs. Sources of biomass substitutes for fossil fuels include plants grown for fuel production purposes in so-called energy plantations, and unused plant and animal residues or solid wastes which are by-products from use of other biotic products. The latter category includes crop harvest residues, animal manure from feedlots, and urban and municipal solid wastes. In spite of the focus on potential energy plantation species here, the importance and value of conversion of organic residues and wastes should not be discounted. As a 1976 National Academy of Sciences study on renewable resources for industrial raw materials noted, the real hope for energy plantations rests with their combined use with these other biomass energy resources. When used in combinations with conversion of other organic residues and wastes, single-crop energy plantations and multiple-use crop operations are more likely to be profitable energy-producing options.

Two of the several ways in which plant biomass can be converted into fuel are: cultivation and "mining" hydrocarbons or plant oils from particular oil- or latex-producing plant species; and cultivation of sugar-producing plants followed by extraction and fermentation of the sugars to ethanol. Either option has the potential to provide an alternative to fossil fuels for energy, particularly in localized economies. Moreover, when they can be grown as multi-use crops on marginal, semi-arid lands, fuel oil plants seem especially promising as alternative energy-producing resources. However, one disadvantage associated with cultivation of biomass for fuel conversion is that annual crops tend to be more productive than perennial crops in terms of biomass production, yet they present postharvesting, storage, and preservation problems. In contrast, perennial crops tend to be less productive, but they can be maintained until they can be harvested. A second problem is that extensive tracts of land are required for each biomass conversion operation, and cultivation of crop plants

for conversion to ethanol, in particular, competes with crop production for human consumption.

Obviously, preference should be given to new crops that are adapted for cultivation in desert, semi-arid, or other marginal environments where food crops cannot be grown without extensive irrigation. Some potential fuel oil- or hydrocarbon-producing candidates include guayule, some *Euphorbia* spp., and a pest species of arid lands, tumbleweed (*Salsola pestifer*). It has been suggested, for example, that tumbleweed could be pelletized for use as a boiler fuel, and that it may have the potential to yield crops worth $790/ha ($320/acre) in desert or semi-arid lands. Yet even though arid land energy crops would not interfere with food crop production, the land required to supply long-term biomass conversion operations would result in the development of large portions of fragile, semi-desert environments that are now being conserved by default. Thus, even though potential energy resources should be developed and exploited, particularly to provide a means of income in resource-poor areas of the world, attention should be first paid to assessment of other genetic resource populations present in these environments. In addition, ecologically fragile areas and prime resource habitats should be located and set aside as arid lands management areas or wilderness reserves, before large-scale energy production projects are instituted which would forever destroy these environments and the alternative resources they harbor.

The investigation of fuel oil plants in the United States actually began shortly after World War I with the investigation of potential U.S. sources of rubber by the inventor Thomas G. Edison. Edison, backed by industrialists Henry Ford and Harvey Firestone and, then Secretary of Commerce, Herbert Hoover, realized that rubber was such an important strategic raw material to the United States that he felt we should develop and produce our own sources of natural rubber. Of the 2,000 U.S. plant species Edison examined, he discovered only one or two (e.g., guayule—an already utilized species that possesses hydrocarbons of large enough molecular weight for it to be useful as a rubber-producing species). Edison was relatively unsuccessful in finding domestic sources of rubber, and he died shortly after he completed this work. However, he had unwittingly discovered numerous domestic sources of "oil" or low molecular weight hydrocarbons.

Recently, Dr. Melvin Calvin, the Nobel Laureate, and a group of USDA scientists lead by Dr. Russell Buchanan have begun to reevaluate Edison's findings and to initiate research on other plant species that could be "mined" for their oil or hydrocarbons. Dr. Calvin contends that green plants can be used to capture solar energy by converting it into energy-rich organic compounds, and that these chemicals can then be harvested and refined or converted into fuel to replace our dwindling fossil fuel resources. He has calculated that production of hydrocarbons in Malaysia from the premier rubber species, *Hevea brasiliensis*, is currently averaging the equivalent of about 25 barrels of oil per hectare (10 barrels per acre) annually. The most productive experimental plots, with trees that have been genetically improved for high yield, could produce as much as 74 barrels/ha per year (30/ac per year). However, he has been focusing his research on other species of hydrocarbon-producing plants that can be grown in the United States, particularly *Euphorbia tirucalli* of Brazil, *Euphorbia lathyrus* of California, and members of the milkweed family (Asclepiadaceae). He believes that even with wild, genetically unimproved plant species, we could produce from 5-25 barrels of oil per hectare (2-10 barrels per

acre) annually. Based on initial cost production estimates of from $15-20 per barrel, oil and chemical companies in the United States and Japan have already initiated the establishment of some *Euphorbia* plantations.

The USDA research group has taken a slightly different approach. Their aim is to locate promising U.S. hydrocarbon- and oil-producing species that can serve as multiple-use crops. In addition to their use as sources of hydrocarbons for fuel, the most promising species they have identified would also provide chemical intermediates. These would include waxes, terpenes, long-chain alcohols, sterols, tannins, rosin, resins, and fatty acids. In addition, many species could also serve as sources of fibers for paper-making, high-protein feed and feed supplements, glucose, vegetable oils and other edible products, and soil amendments. Some of the native U.S. rubber-producing species that might be used as plantation crops for production of fuel hydrocarbons as well as other products are listed in Table 1.

Most of these species are perennials which could be harvested as needed. All of them possess significant levels of tannins (polyphenols), chemical compounds that were once used extensively for tanning leather. Recently, however, interest has been renewed in low-cost polyphenols for plywood glues and particleboard adhesives, oil-well drilling muds, wood laminating resins, antioxidants, and various other uses, including controlled-release substances for fertilizers and pesticides. Many of these plants also contain significant levels of waxes or natural rubber, both of which have a variety of industrial applications. Furthermore, some of these species, e.g., New Jersey tea, wild plum, pokeweed, ironweed, common elder, smooth sumac (Fig. 1) and sassafras, are known for their edible or medicinal uses. Genetic improvement for increased oil or hydrocarbon production might reduce the latter potential uses of

Fig. 1. Smooth sumac *(Rhus glabra),* still valued as an edible and medicinal plant, also shows potential as a fuel oil plant. (Photo: U.S. Forest Service, USDA)

TABLE 1. Native U.S. Plants Under Investigation As Potential Fuel Oil Crop Species

Latin Name	Common Name	Crop Type	% Oil	% Wax	% NR	% Wax* & NR	% Unident.** Hydrocarb.
Aceraceae	Maple family						
Acer saccharinum	Silver maple	Oil	2.29	—	—	—	0.38
Anacardiaceae	Cashew family						
Rhus glabra	Smooth sumac	Oil	5.51	0.20	—	—	—
Campanulaceae	Bellflower family						
Campanula americana	Tall bellflower	Oil & NR	6.07	—	—	0.93	—
Caprifoliaceae	Honeysuckle family						
Sambucus canadensis	Common elderberry	Oil & NR	2.13	—	0.50	—	—
Symphoricarpos orbiculatus	Coralberry	Oil & NR	2.19	—	0.77	—	—
Compositae/Asteraceae	Sunflower family						
Ambrosia trifida	Giant ragweed	Oil & NR	7.60	—	0.55	—	—
Crisium discolor	Field thistle	Oil & NR	5.24	—	—	0.36	—
Eupatorium altissimum	Tall boneset	Oil & NR	5.52	—	—	0.52	—
Silphium integrifolium	Rosinweed	Oil & NR	2.52	—	0.70	—	—
Silphium laciniatum	Compass plant	Oil & NR	3.00	—	0.68	—	—
Silphium terebinthinaceum	Prairie dock	Oil & NR	2.49	—	0.85	—	—
Sonchus arvensis	Sow thistle	Oil & NR	5.32	—	—	0.72	—
Vernonia fasciculata	Ironweed	Oil & NR	5.01	—	0.36	—	—
Euphorbiaceae	Spurge family						
Euphorbia dentata	Lechillo	Oil	9.68	—	—	—	0.17
Euphorbia lathyris	Mole plant	Oil	9.21	—	—	—	0.37
Lauraceae	Laurel family						
Sassafras albidum	Sassafras	Oil	5.55	0.22	—	—	—
Phytolaccaceae	Pokeweed family						
Phytolacca americana	Pokeweed	Oil	3.41	—	—	—	0.17
Rhamnaceae	Buckthorn family						
Ceanothus americanus	New Jersey tea	Oil	3.27	0.64	—	—	—
Rosaceae	Rose family						
Prunus americanus	Wild plum	Oil	3.93	—	—	—	0.17

Source: Buchanan and Otey, 1978.
*Waxes and natural rubber (NR) were included together as one fraction for some plants.
**For some plants, hydrocarbons were unidentified.

these species. However, other possible uses, such as fiber or extractive protein production, could probably be retained as they are selected for higher production of specific hydrocarbons or whole plant oils.

In contrast to the strategy of cultivating and harvesting plants directly for their hydrocarbons and oils, we can also obtain energy by fermentation of sugars from such edible plants as maize (*Zea mays*), sorghum (*Sorghum bicolor*), sugar cane (*Saccharum officinarum*), and cassava (*Manihot esculenta*). Some edible domesticates, e.g., maize, sorghum, and sugar cane, are "C-4" photosynthetic plants. C-4 plants have virtually eliminated the need for photorespiration; they are generally capable of higher net photosynthesis rates under conditions of bright sunlight than even the most active C-3 plants. At present, sugarcane is the most promising C-4, sugar-producing species used for fermentation to fuel alcohol. In recent years, Brazil has been the world's largest cane sugar producer, producing 6-8 million tons per year. Brazilians have traditionally obtained ethanol (ethyl alcohol) by fermenting surplus molasses and cane residues from sugar manufacture. The ethanol obtained has been used primarily as a gasoline fuel additive, and the percentage of ethanol in their gasoline has varied from 2-15 percent over the years. Moreover, its use as a fuel oil has some advantages over petroleum; when added to gasoline, it increases fuel octane ratings and reduces engine knock, thus obviating the need for lead additives. Ethanol-powered engines produce smaller quantities of other pollutants, and ethanol also produces 18 percent more power than gasoline.

Ethanol production in Brazil in the early 1970's averaged 570-700 million liters annually (150-185 million gal). In order to encourage ethyl alcohol production, the government instituted measures to ensure that equal monetary returns could be obtained from either 90 kg (198 lb) of sugar or 30 liters (8 gal) of alcohol—both of which can be produced from 1 ton of sugar cane. The purpose of this pricing policy was to aid in the development of biomass production of liquid fuels. In recent years, about 80 percent of Brazil's energy needs have been supplied by imported oil, at an annual cost of over $3-5 billion. In order to achieve greater self-sufficiency in energy production and use, a national goal was set to eventually obtain 75 percent of all liquid fuels from sugar cane or other sources of fermentation sugars. To meet these goals, plans were made to construct and operate new alcohol distilleries, and to produce automobiles with engines geared specifically for ethanol use.

The past success of the ethanol production program in Brazil and its current ambitious plans to attain near self-sufficiency in energy production offers hope for many of the less technologically advanced countries in the tropics. Tropical countries receive an overabundance of incident radiation from sunlight, and this radiant energy can be converted into energy-rich sugar compounds by plants for alcohol fermentation. Greater use of sugar crop residues and any excess crop productivity for alcohol production could provide an important alternative source of energy for some tropical nations which do not have significant fossil fuel reserves.

In contrast to the fuel alcohol production potential of the tropics, most temperate areas suffer from a variety of limitations on this biomass conversion option. One limitation is that few countries, including the United States, possess significant amounts of land suitable for cultivation of sugar cane, cassava, or other sugar crop species. At present, the best option for the United States is maize. Moreover, most land suitable for crop cultivation in the United States is already being utilized; and, cultivation of crops for alcohol fermentation will compete with use of

agricultural lands for crop and livestock production. High land rental and labor costs compound the problems faced by fuel alcohol production operations. Yet, as petroleum and other fossil fuel costs continue to soar, the use of agricultural lands for fuel oil crop production may prove to be more economically efficient than production of food crops. It remains to be seen whether this possibility will occur, or whether the United States and other temperate nations will take the opportunity instead to domesticate and cultivate new, noncompeting, arid lands crops. At this point in the development of the biomass conversion industry in the United States, either option might be adopted.

The preliminary results of these ongoing research projects to discover new crops for biomass conversion demonstrate the importance of conserving both germplasm resources (*ex situ*) and genetic reservoirs (*in situ*) of such wild and weedy plant species. Development of crops for oil and hydrocarbon production will require exploitation of new germplasm resources, and hence new gene pools. Use of major crops for production of fermentation sugars will necessitate some genetic improvement of current domesticates for their specific task of producing higher quantities of sugar. In addition, emphasis on use of germplasm resources to convert annual sugar crops to perennials would be useful. One exciting and distinct possibility is that of crossbreeding maize with perennial wild teosinte (*Zea diploperennis*), an endangered form of the closest wild relative of maize (corn). Certainly, as societal needs and values continue to change, new crop plants and their associated germplasm resources will assume economic prominence as their unique attributes become important to us. But in the absence of adequate sources of genetic diversity, domestication of new crops or genetic improvement of extant cultivated species through use of an impoverished gene pool would be a much more lengthy and difficult process. For this reason, endangered species and subspecies within genera that contain oil-bearing plants, e.g., *Asclepias, Solidago, Rhus,* and *Cirsium,* should receive special attention.

Jojoba Oil: An Economic Substitute for Sperm Oil

In 1939 three patents were issued to H. G. Smith which collectively describe one of the most important discoveries in the history of industrial lubricants. These patents heralded the discovery of sulfurization of sperm oil from the sperm whale, *Physeter catodon (= macrocephalus).* The discovery that sulfurized sperm oil was superior as an extreme pressure lubricant or lubricant additive to sulfurized lard or mineral oils led to the annual importation of 9.1 million kg (20 million lb) of the oil for use in gear oils, locomotive and steam cylinder oils, and many other industrial lubricants. By the late 1960's U.S. imports of sperm oil had risen to an average level of 26 million kg (58 million lb) per year. Until 1970, the United States was the largest importer of sperm oil and spermaceti, a hard wax which serves as an economic substitute for the costly carnauba wax from a Brazilian palm.

The economic value of sperm oil can be attributed to its superiority as an anti-rust and anti-corrosion lubricant. Since the 1940's, sulfurized sperm oil has been the premier lubricant for heavy-duty industrial machinery and automobile transmissions. It has also been indispensible as a breaking-in oil for automobile engines, and was employed in all automobiles manufactured in the United States before 1972. It is so valuable as an industrial lubricant, that like rubber and certain timber products, it

has been stockpiled in the event of a national emergency. During 1955-1959 the value of U.S. imports of sperm oil averaged $6.8 million annually for 21.6 million kg (47.7 million lb). By 1961, imports had increased to over $9 million for nearly 30 million kg (66 million lb). The annual value of world production of sperm oil is more difficult to estimate. However Table 2 shows the total value of world production for a 23-year period based on U.S. wholesale import prices. Fig. 2 illustrates total world production from 1952 to 1972.

By the late 1960's evidence of the depletion of sperm whale stocks was accumulating, and conservationists were alarmed by the impending extinction of some

TABLE 2. Estimated Value of World Sperm Oil Production Based on U.S. Import Prices, 1952-1974

Year	Total World Production of Sperm Oil - kG*	Price Per kG**	Total Value in U.S. $ (Rounded)
1952	76,023,150	.3308	$ 25,144,700
1953	51,674,050	.2756	14,242,700
1954	73,015,680	.2701	19,722,400
1955	91,718,060	.3142	28,819,000
1956	110,688,700	.3197	35,389,900
1957	100,240,670	.3252	32,602,000
1958	123,281,280	.3308	40,781,400
1959	117,568,430	.2811	33,052,900
1960	110,624,780	.2701	29,881,100
1961	109,366,100	.3032	33,158,400
1962	121,741,250	.3308	40,272,000
1963	144,320,480	.3418	49,325,100
1964	152,703,690	.3170	48,402,300
1965	141,543,700	.2839	40,183,400
1966	148,232,010	.2756	40,856,400
1967	150,226,450	.2756	41,406,200
1968	121,112,080	.2867	34,716,800
1969	130,475,850	.3969	51,785,900
1970	137,464,210	.3969	54,559,500
1971	122,625,080	.5568	68,273,000
1972	98,118,900	.5568	54,628,900
1973	105,318,060	.4631	48,767,500
1974	100,539,360	.5513	55,422,300
Total Estimated Value of World Production, 1952-1974			$921,393,800

*Production figures taken from Hvalradet—*International Whaling Statistics;* number of barrels were converted to kilograms using the conversion factor of 170 kg/barrel.

**Price per weight figures were taken from the *Oil, Paint, and Drug Reporter: Hi-Lo Chemical Price Issue* (p. 284, for 1952-61) published by the Schnell Publishing Company, Inc. (1962), and from price data (for 1961-74) as provided by Schnell Publishing Company (1980). Prices per kilogram were calculated by converting prices per pound, the latter of which were determined by averaging the high and low prices recorded during each year for natural (unbleached) winter sperm oil in tanks.

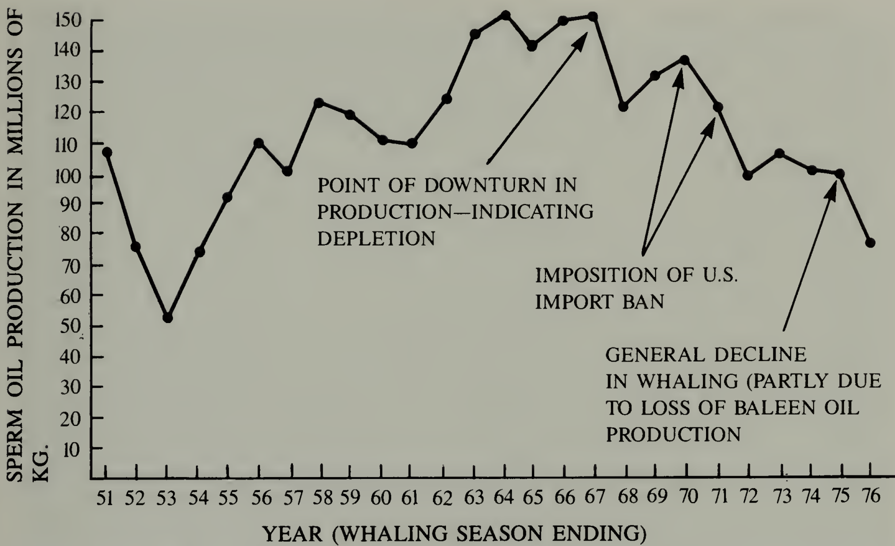


Fig. 2. World production of sperm oil, 1951-1976.* (Source: *International Whaling Statistics)*
*Number of barrels produced × 170 KG. barrel of oil.

of the edible oil-producing whale species that were still being commercially exploited at that time. The pattern of sperm oil production began to decline, in a fashion similar to the downturn observed previously for edible whale oils (see Figs. 8-9, Chapter 3). Thus, the species was finally protected by the Endangered Species Act of 1969 (Public Law No. 91-135, 83 Stat. 275, 1969; repealed by Endangered Species Act of 1973, as amended, 1979). An import ban on sperm oil and spermaceti (a hard wax) was imposed late in 1970, with special permits allowing an additional 20.7 million kg (45.6 million lb) to be imported during 1971. Since 1970, sperm oil has been rationed from the U.S. strategic stockpile for vital industrial needs. However, by 1976 stockpiled sperm oil was reported as selling on the market at $1.21/kg (about $0.55/lb), while on the black market it was reputed to be fetching prices as high as $2.20/kg ($1.00/lb). In comparison, U.S. import prices actually decreased from 1952 to 1960, going from $0.33/kg ($0.15/lb) to $0.27/kg (about $0.12/lb). Thus, prices for sperm oil apparently increased after the imposition of the U.S. import ban, reflecting the increased economic scarcity of the product in this country. In spite of the U.S. ban, whalers, primarily from the Soviet Union and Japan, continued to harvest from depleted sperm whale populations, and produced an average of 50-54 million kg (110-119 million lb) of sperm oil annually between 1970 and 1977. In addition, pirate whalers have been harvesting animals from sperm whale populations during the last decade.

A fortunate result of the import ban has been an upsurge of interest in a terrestrial U.S. desert plant, jojoba (*Simmondsia chinensis,* Simmondsiaceae) (Fig. 3) which can provide an economic substitute for sperm oil. Jojoba oil was first suggested as a sperm oil equivalent as early as 1936, 3 years prior to Smith's discovery of the potentials of sulfurized sperm oil. A U.S. patent for sulfurization and hydrogenation of jojoba oil was granted in 1942. On the basis of performance

Fig. 3. Jojoba *(Simmondsia chinensis),* an arid-adapted plant of the southwestern U.S. which yields fruits ("beans") that contain jojoba oil. (Photo: M. Oldfield)

evaluations, both of the sulfurized oils show nearly equivalent properties in lubricant applications. In contrast, base mineral oils and sulfurized lard oils are inferior as lubricants, as are the petroleum-based synthetics employed after the U.S. import ban on sperm oil. In fact the use of inferior sperm oil substitutes caused some problems for industry. As an example, General Motors was forced to recall 5,500 automobiles and carry out over $2,000,000 worth of repairs because an inferior lubricating oil substitute caused antifreeze leakage into transmissions and oil leakage into radiators.

In comparison, sulfurized jojoba oil is nearly equivalent to sulfurized sperm oil in lubricant function, and it actually has several advantages over it. It has a pleasant, mild odor, contains no glycerides and very few other chemical impurities, and requires little or no refining for many of its most important uses. Moreover, it can be harvested from a land-based plant resource well adapted for cultivation in semi-arid desert regions. In addition to these advantages, jojoba has many other useful attributes. It produces a naturally pure oil which contains unsaturated hydrocarbons and has a relatively simple molecular structure. The oil is highly stable, nondrying, and resistant to oxidation; thus it can be stored for years in seed or as a refined oil without becoming rancid. It has a high viscosity index, high fire and flash points, and a high dielectric constant—properties which make it favorable for select industrial applications.

In addition to its use as a sperm oil substitute, jojoba oil has a variety of other uses (Table 3). When it is hydrogenated, it can serve as an economic substitute for spermaceti wax (hydrogenated sperm oil) or for "the king of waxes," carnauba wax. Thus it can be used in furniture, auto, and shoe polishes, carbon and stencil paper, insulating materials, and film coatings for fruits and vegetables, as well as for a myriad of other industrial uses of carnauba wax and spermaceti. Although hydrogenated jojoba oil is not equivalent to carnauba wax in hardness, jojoba seeds yield much more oil for conversion to wax than carnauba palm leaves can provide as pure wax. Moreover, cultivation of jojoba will not only provide an economically competitive source of hard waxes (in 1975, carnauba wax sold for $4.50/kg, or $2.05/lb). But it may also lessen the harvesting impact on slow-growing carnauba palms (*Copernicia cerifera*) in Brazil, and on Mexican candelilla wax shrubs (*Euphorbia antisyphilitica* and *Pedilanthus pavonis*) which must be sacrificed for wax production. These hard wax-producing, wild plants have all suffered from overexploitation in the past.

In the pharmaceutical industry, jojoba has many potential applications. It is proving to be a superior antifoaming agent for production of antibiotics. In comparison with sperm oil, only one-sixth as much jojoba oil is needed for penicillin fermentation, and only half as much is required for fermentation of cephalosporin. Thus in comparison with known antifoaming animal oils, use of jojoba oil for microbial fermentation processes is more economical. It has been estimated that only 2,650,000 liters (700,000 gal) of jojoba oil would be required to produce penicillin for current world needs. Jojoba oil is also being investigated for use as a "carrier" of penicillin and vitamin A compounds. Since the oil is believed to be indigestible by humans, it may enable such medicinal compounds to pass, undigested, through the stomach to the small intestine. It has also shown promise for treatment of acne and other excessive secretions from sebaceous glands. Numerous herbal and cosmetic uses of the plant by the Indians of Baja California and the Sonoran desert region have been recorded.

TABLE 3. Jojoba Liquid Wax: Current or Potential Uses

Treatment of Jojoba Liquid Wax	Actual or Potential Uses of Wax
Untreated or sulfurized pure wax	Substitute for sperm whale oil Lubricants and lubricant additives Cutting, drawing, and grinding oils Transformer oils Pharmaceutical and cosmetic uses Cooking/dietary uses
Hydrogenated liquid wax	Carnauba wax substitute Ingredient used in: floor finishes, furniture, auto, and shoe polishes carbon and stencil paper Additive to waxes used in: paper and matches textile sizings insulating materials batteries candles and candle-coatings soap chalk and crayons salves and pharmaceutical creams film coatings to retard food spoilage bakery release agents and lubricants lipstick and cosmetic products
Treatment with sodium chloride	Factices for production of; varnishes rubber adhesives linoleum printing ink
Treatments of alcohols and acids derived from wax conversion or present in liquid wax	Used directly or as an intermediate for: lubricants emulsifiers antifoaming agents for antibiotic fermentation processes bases for ointments and creams Intermediates for preparation of: disinfectants detergents surfactants driers emulsifiers resins plasticizers and stabilizers protective coatings fibers corrosion inhibitors Adhesives

Sources: Spadaro and Lambou, 1973; NAS, 1975.

Aside from its pharmaceutical importance, jojoba has many other potential applications in industry. Its indigestibility warrants further investigation for use in the production of low-calorie foods and diet products. Because it does not become rancid, it is a promising oil for the cosmetics industry. Jojoba nut meal, a by-product after oil extraction, may become a supplemental livestock feed for nearby arid rangelands. It contains fiber, carbohydrates, and 25-35 percent protein. However, this use of the jojoba plant may be possible only after further research on detoxification of simmondsin, a toxin present in jojoba seed which might be made nontoxic by treatment with ammonia or some other chemical.

Because jojoba is a multi-use plant that may be used in manufacturing, pharmaceutical, cosmetic, and other commodities, it has much potential as a new crop species. The decline of the whaling industry as a result of the overexploitation of edible whale oil species combined with the impact of the U.S. import ban on inedible whale oil from the sperm whale has given new impetus to the development of jojoba as a cultivated crop. Jojoba has many virtues for development as a domesticated crop plant. One is that its seeds provide a highly concentrated source of the valuable oil; they average 50 percent liquid wax, varying from about 43 percent to almost 59 percent. Other plant species which produce oilseeds that yield valuable wax-esters, such as colewort or Abyssinian kale (*Crambe abbyssinica*) (Fig. 4) and meadow foam (*Limnanthes* spp.), possess lower percentages. Through genetic improvement, high-yielding jojoba varieties should be able to produce oilseed with at least 60 percent wax. Secondly, because jojoba is an endemic of the Sonoran desert region of Mexico and the southwestern U.S., it is heat- and drought-resistant. It is capable of tolerating temperatures in the shade in excess of 43-46 °C (110-115 °F). And it can survive on less than 12.7 cm (5 in.) of rain annually, although 38-46 cm (15-18 in) in winter and spring are required for optimal seed production. Jojoba is also tolerant of salty, alkaline soils that are typical of most desert and semi-desert regions. These attributes will make jojoba an important crop plant for resource-poor nations that have large areas of semi-arid lands.

For example, jojoba has been successfully cultivated in desert regions of Israel. Its potential use for cultivation on Indian reservations in the Sonoran desert region of the United States promises to enhance the local economies of that area. As a crop plant, jojoba will provide an important alternative for agricultural areas that are presently consuming huge quantities of water for irrigation. As an example, on a per unit area basis Arizona's irrigated crops (sorghum, cotton, etc.) currently consume about 2.4-3.0 m (8-10 ft) of water annually, and crop irrigation accounts for roughly 90 percent of that state's total water consumption. In contrast, a jojoba crop would consume less than 0.3-0.45 m (1-1.5 ft) of water per unit area per year for commercial production. More efficient use of diminishing groundwater resources is an extremely important issue in the western United States. Overuse of available groundwater resources for irrigation by one state or area can impose external economic costs on other states or regions in terms of lowered crop productivity and increased pumping expenses. Current demand on aquifers might be significantly reduced by development and cultivation of more suitable arid lands crops like jojoba or guayule; and this may, on an overall basis, slow the degradation of arid land resources caused by too rapid withdrawal of groundwater reserves.

Although cultivation of jojoba may provide a partial answer to irrigation problems and state conflicts over water rights, can it even begin to supply sufficient quan-

Fig. 4. Colewort *(Crambe abyssinica)* seeds contain approximately 20 percent of the desired glycerides which are used for making industrial lubricants, rubber additives, synthetic fibers and plastics, oils for formulating waxes, and other chemical raw materials. (Photo: Agricultural Research Service, USDA)

tities of oil to meet current world needs for sperm oil? It has been estimated that about 136 million kg (300 million lb) of jojoba oil, about equivalent to the level of sperm oil production in the late 1960's, will be required to replace current world demand for sperm oil. Production estimates suggest that shrubs producing adequate yields could individually supply 2.3 kg (5.1 lb) of oil annually, with the number of shrubs per hectare ranging from 250 to 800 plants (100-325/acre). Depending on how many plants can be cultivated per unit area, 73,650-242,820 ha (182,000-600,000 acres) will be required to meet world needs, and 14,160-46,940 ha (35,000-116,000 acres) will be necessary to meet U.S. demand. Although these production estimates on a per unit area basis are much greater than those obtained from unimproved, natural stands, it is clear that jojoba must be domesticated and developed as a plantation crop if jojoba oil is to replace sperm oil as an indispensible industrial lubricant.

Even in its genetically unimproved state, jojoba appears to be commercially attractive as a plantation crop to meet U.S. needs. Yet the future of the jojoba industry rests on its potential for domestication. This means that genetic improvement of the plant will be necessary. To this end, a jojoba germplasm resources collecting expedition was conducted in 1977. Emphasis was placed on collection of germplasm for: large-seeded plants; cold-hardiness; tall, upright habit; and abundant and fascicled (many-seeded) fruiting. In addition to selection for these traits and higher wax content (yield), emphasis must be placed on aspects of oil quality, early maturation of plants for enhanced production, and greater salt tolerance. Susceptibility of the plant to various diseases and pests must be adequately assessed, and germplasm resources to provide needed resistance or tolerance to these pests must be located and evaluated.

If we are to reduce the economic impact of future world demand for a unique and indispensible industrial lubricant on depleted sperm whale populations, and to develop native American alternatives for production of such oil products, now is the time for cultivation and development of jojoba as a crop. Therefore we must continue to support projects such as the Indian reservation production systems in the Sonoran desert region, and we must set aside other semi-arid areas suitable for cultivation of the plant. Jojoba offers the additional advantage of being able to aid in the development of many resource-poor desert regions where livestock production currently overstresses fragile desert ecosystems.

8
Wild Biota and Other Economic Activities

International Trade and Endangered Species

Wildlife is the mainstay of some business enterprises within the fashion and wearing apparel industries, the souvenir (tourist curios) trade, and the burgeoning trade in live plants or animals and wildlife products. However, consumer demands for wildlife or the luxury goods produced from wild species is today a major cause of extinction or endangerment of such economically valuable biota, and for a great many species, it is the leading cause of their impending extinction. Trade in endangered or rare, unique or unusual wildlife or their derived products is a disproportionately lucrative business in comparison with trade which centers on more abundant, commonplace, or less interesting taxa. For example, from 1967 to 1968, roughly 42,000 reptiles and amphibians, 547,000 birds, and 31,000 mammals were traded internationally to pet dealers and to a lesser extent to research institutions and zoos, at a value of $1.9 million. However, $1.7 million (nearly 90 percent) of these sales were attributed to only 38 percent of the live animals traded; for the most part, these were the more rare or unusual species. Similarly, although furs from the large, spotted cats accounted for less than 1 percent of the volume of furskins traded in the late 1960's, the value of the spotted cat trade amounted to 8.5 percent of the total trade.

Although most highly valued but endangered species which enter international trade are threatened by a variety of human activities, the tremendous prices that consumers—primarily those in the more affluent nations—are willing to pay for exotic pets, beautiful or unique furs, or other fashion or luxury items has been a major factor contributing to the demise of most such wild species. Many wild plant species can be easily cultivated and some animal species are adaptable to life in captivity; when such taxa become vulnerable to extinction, they can and should be propagated to provide a sufficient supply of the desired product(s) to meet market demands. Un-

fortunately, it is usually cheaper, easier, or more convenient to extract specimens from the wild (and use the free work of nature to produce them) than it is to financially support captive or cultivated breeding populations of useful or valuable species. As a result, the economic productivity of most wildlife-based industries still tends to be sustained primarily by wild populations—frequently until they are driven to the brink of extinction.

In order to prevent overexploitation of particularly vulnerable species, it is essential to implement and enforce both domestic legislation in producer and consumer nations and international treaties designed to monitor and regulate international trade in such species. Appropriate examples include U.S. legislation such as Endangered Species Act of 1973 (as amended) and the Lacey Act, and treaties such as the Migratory Bird Treaty and the Convention on International Trade in Endangered Species of Wild Fauna and Flora, commonly known as CITES. CITES, in particular, was only recently instituted; it came into force in 1975, and by December 1982, it had been ratified by 78 member nations, including nearly all of the major wildlife consuming nations, e.g., Japan, China, the United Kingdom, the United States, and West Germany. CITES has already begun to curb the threat of extinction for the hundreds of threatened species traded internationally that are currently listed for monitoring and protection via its special permit system. Yet despite progress it is still beset with many problems. Many nations that produce or consume products from threatened wildlife species have not signed the Convention (e.g., Taiwan), while others have done little to abide by or actively enforce it. Moreover, the Convention allows signatory nations to take reservations on particular species; for example, Japan has taken reservations on all three endangered species of sea turtles listed in the Convention and still imports sea turtle products; and Italy and France have taken reservations on three of the four crocodile species listed for protection under Appendix I. As more nations join the Convention and as more member nations endeavor to implement and effectively enforce it, CITES promises to do much to lower the accelerating pace of human-induced extinctions and to protect our global genetic heritage for future as well as present generations.

Aside from ratification and enforcement difficulties with CITES (and other extant conservation legislation), other problems invariably arise whenever rare or endangered taxa are traded domestically or internationally. When trade bans are imposed on products in great demand (because consumers perceive them to be highly valuable), illegal trade activities and black market operations inevitably fill the gap. In reality, enforcement of laws designed to regulate the supply of such products is usually expensive and, in a practical sense, difficult to achieve. In many areas of the world, the money offered by commercial dealers for one or only a few furskins from an endangered species is sufficient to support the hunter-collector and his family for an entire year. When few alternative occupations are available, as is the case in many of the developing nations where a great proportion of these endangered species reside, it becomes relatively easy to understand the strong economic incentives which encourage poaching operations. Moreover, smuggling endangered wildlife or their derived products has become generally more profitable and less hazardous (in terms of penalties and fines) than smuggling narcotics. Since the illicit wildlife trade has become a multibillion dollar business worldwide, many game wardens, wildlife managers, and law enforcement personnel have lost their lives in the battle to curb poaching and smuggling. In short, wildlife managers and conservationists are caught

in a double bind: If trade bans on endangered species are not imposed, legal trade activities will tend to proceed until species near or reach extinction; if they are imposed—without simultaneous reductions in consumer demand—the prices paid for the wildlife or items made available in illegal markets will be sufficiently high to encourage the exploitation to continue anyway.

This dilemma highlights the important role that individual consumers play in current conservation efforts. If more consumers were aware of their role in the extinction process, and more willing to take responsibility for that role, e.g., by voluntarily reducing their demand for products derived from wild-caught specimens of threatened species, the survival of many endangered taxa would be ensured (at least with respect to threats due to trade), and the financial and social costs of enforcing needed conservation laws would be considerably lessened. However, until consumers change their attitudes about consumption of endangered wildlife or their products, the supply flow, and hence the confiscations and seizures of illegally obtained wildlife commodities, will continue. The wild populations from which these goods were derived will continue to decline, and an ever-increasing number of highly valuable or unique species will continue to be irretrievably lost—never to be seen or enjoyed by future generations. Despite CITES and other forms of conservation legislation, nothing can be done to resurrect the organisms sacrificed to meet consumer demands for the illegal wildlife trade. Although U.S. Customs warehouses, such as the room of confiscated goods depicted in Fig. 1, will not be filled as quickly as they were being inundated prior to the adoption and enforcement of CITES, the slaughter of endangered wildlife will nevertheless continue through clandestine trade operations as long as affluent consumers sustain their demands.

The relationship between consumer demand and the wildlife extinction process is strongly tied to the nature of consumer psychology. Frequently, when consumers perceive the uniqueness or rarity of a particular species or one of its products, they are willing to pay much higher prices than they would for functional goods which could be used as economic substitutes, yet which are less interesting, unique, rare, or "authentic." If the species is not capable of reproducing and thus replenishing its populations faster than they are being exterminated, it will inevitably become endangered or extinct in the absence of effective control over the supply-demand process. Once commercial demand has become well established for an unprotected, rare, or unique species, a continuous spiral of demand-supply interactions often occurs until the species becomes endangered or extinct in the wild (Fig. 2). As the perceived value of a species increases from the consumer's perspective—a perception enhanced all the more by its ever increasing scarcity or rarity as the depletion process continues—wholesale import dealers will front more money to cooperating export dealers. The export dealers, who coordinate or interact with persons involved in the clandestine poaching and smuggling operations that concentrate on endangered wildlife species, are then able to offer greater economic incentives to the hunter-collectors who must ultimately search for the increasingly fewer individuals that remain in the dwindling population(s).

Examples of this process are legion, even though very few cases have been well-documented. Consider the impact of the fur craze of the late 1920's and early 1930's on the wild chinchilla (*Chinchilla laniger*) populations of South America. During that period, European furriers could obtain as much as $100,000 for a single coat made from wild chinchillas—a very handsome price in those days. Demand for chin-

Fig. 1. A U.S. Customs storeroom in New York City filled with confiscated products derived from endangered species. (Photo: S. Hillebrand, U.S. Fish and Wildlife Service, USDI)

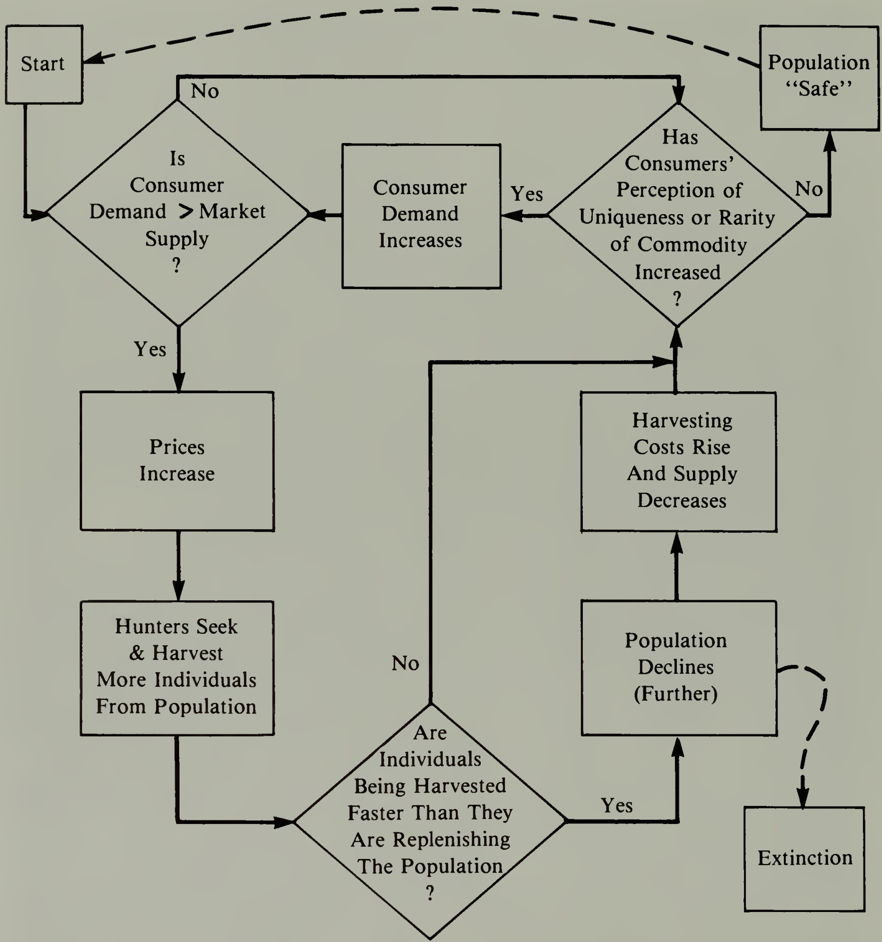


Fig. 2. Relationship between consumer psychology and the market pricing mechanism for a rare or unique wildlife commodity.

chilla furskins became so great that fur buyers in Europe instructed their foreign agents to acquire chinchilla pelts at any price; trappers completely exterminated chinchilla populations in the lower altitudes of the Andes Mountains, and by 1943 only a few isolated colonies remained. The chinchilla, however, has been more fortunate than a great many other fur-bearing animals. In comparison with most mammals valued in the fur trade, it has a relatively high reproductive capacity, and has adapted well to captivity—so well in fact that commercial breeders can now easily produce sufficient numbers of pelts to meet present consumer demand. Additionally, changing trends within the fashion industry and the passing of the fur craze during the earlier part of this century also significantly lessened the impact on wild populations. Today, especially in Chile where protective legislation has been instituted, many wild chinchilla populations are recovering.

However in the face of intense consumer demand, most wild animal and plant species are incapable of reproducing and growing fast enough to provide a sufficient supply of the desired product(s). As the distinct populations or subspecies become exterminated, the unique gene pool resources each represents and, eventually, the entire species will be lost. Careful study of the voluminous list of species threatened principally by trade in wildlife products reveals that a great proportion are slow-maturing. Moreover, once individuals reach maturity, they typically produce less than one to a few offspring per year. Thus, even though all wildlife species or populations are potentially renewable resources, some are much less capable of favorably responding to harvesting pressures than others. Dr. Colin Clark, a bioeconomist, has provided a mathematical proof of a theorem which states that whenever the prevailing discount rate of a harvesting firm exceeds twice the reproductive potential of the exploited species, normal harvesting processes will inevitably induce the extinction process. Clark initially developed his bioeconomic analysis for the blue whale (*Balaenoptera musculus*), which yields an edible oil (Chapter 3). Using the estimated maximum reproductive rate of 4-5 percent per annum for the blue whale (about one offspring every 2 years with good adult survival rates), he concluded that the discount rate within the whaling industry should not have exceeded 8-10 percent per annum in order to prevent depletion or extinction of the available stocks. Unfortunately, discount rates in the private sector of most industries have exceeded 10-11 percent in recent times, and within the whaling industry, the prevailing rate is believed to have been higher than usual. When discount rates are high, as in the case of extraction of virgin timber resources (Chapter 5) investors will prefer to liquidate the resource stock (as a form of capital) and invest the revenues obtained from disinvestment of the stocks elsewhere. Thus, when market discount rates are high, the tendency is to rapidly discount the value of expected future returns or productivity that would otherwise accrue from preservation of a sufficient-sized breeding population and stock management. Under such circumstances, economic, if not biological, extinction should be expected. Similar conclusions could be drawn from other highly valuable, but slow-maturing species which produce less than one or a few offspring per year, e.g., many non-human primates (research subjects), elephants (ivory), rhinos (rhino horn), and the larger cats and other fur-bearing carnivores. In these demand-supply situations particularly, protective legislation often has the unintended effect of increasing prices for the commodities by decreasing market supplies even further than they are being diminished due to increasing biological scarcity. It therefore indirectly facilitates consumers' perceptions of enhanced value or rarity of the commodities in question. As long as people *perceive* that the value of a particular wildlife species or its products has increased (relative to other goods), they will pay inflated prices for such commodities. Poaching of protected species or the unrestrained slaughter of more abundant and unprotected species will therefore continue to threaten their survival. This process is one of the more important mechanisms by which the desires of affluent consumers indirectly contribute to the extinction process.

The fact that some species are biologically more vulnerable to extinction than others is an issue that must be reckoned with whenever a renewable, living resource species is exploited for economic purposes; and the issue of natural reproductive capacity is only one of many considerations. However, rather than adopting the view that it is the vulnerable species that are at fault due to their evolved physiological,

behavioral, or other capacities, we as a predatory species must begin to alter our harvesting policies to incorporate the biological aspects of their evolutionary histories which necessarily impose limitations on our use of such species. During the last few decades, much progress has been made toward studying these biological limitations. However, considerably less progress has been made toward countering human-induced causes of extinction through attempts to alter the more flexible behavior patterns of the consumers and producers of wildlife products. Whenever a rare or unique species falls into the demand-supply spiral (Fig. 2), there is no escape from the trend toward depletion or extinction in the wild in the absence of effective legal protection, unless: (1) captive/cultivated breeding stocks are established, and sufficient numbers of animals or plants are artificially propagated to meet market demands or significantly reduce pressures on the wild populations; or (2) most of the consumers (either retail or wholesale) voluntarily terminate or reduce their demand for the wild species or its products. Given the biological limitations with which we must contend when renewable resource populations are being exploited, both of these options should be more fully explored and developed as conservation strategy alternatives than they have in the past.

The first alternative of appropriating breeding stocks for purposes of establishing captive/cultivated resource populations is one of the important ways in which we can more fully utilize the biological resources harbored within *in situ* conserved natural areas. In addition to the chinchilla example, many rare tropical orchids and other wild plant species have been successfully extracted from natural environments and propagated in sufficient quantities to meet market demands. Moreover, "farming" or "ranching" of captive stocks of the green sea turtle, some crocodile species, and some of the rare and beautiful birdwing butterflies is now being conducted experimentally in parts of the world. However, for most wild animal species and plant taxa, especially those which have exacting life requirements or specific habitat preferences, captive breeding has proved thus far impossible or impractical. Furthermore, the proliferation of supposedly captive-bred or -propagated stocks of threatened taxa on the market often makes regulation of trade in wild-caught specimens difficult or impossible to achieve, expecially in the absence of permanent or indelible marking techniques which cannot be easily duplicated by poachers and smugglers. Additionally, survival in captivity alone is not equivalent to survival in the wild; and a species which is extinct in the wild must be considered, for all practical and immediate purposes, ecologically (if not economically) extinct. Unfortunately, the captive-breeding option all too often is instituted immediately prior to extinction or severe depletion, rather than being adopted as an option to prevent or inhibit extinction.

The other alternative—encouraging consumers to voluntarily reduce their demand for endangered species or their products—is not a commonly attempted option for a number of reasons. Most important, perhaps, is the diffuse nature of the demand process coupled with "imperfect" rather than "perfect" knowledge on the part of individual consumers. Even if consumers have full knowledge of the conservation status of the species they value and of their role in the consumption/extinction process, it is difficult to organize a concerted effort to encourage adequate reductions in demand in order to effect conservation. Despite these problems and the paucity of previous experiences with this approach, sociocultural mechanisms for reducing consumer demand have been and can be very effective in accomplishing

needed conservation objectives. As an example, consider the decline in popularity of feather millinery fashions in the early 1900's in response to the detrimental impact of the feather fashion craze of the late 1800's on many bird species. During this fashion fad, a great variety of birds was harvested for the feather trade, including pheasants, ostriches, hummingbirds, birds of paradise, herons and egrets, parrots and other psittacines, pigeons, doves, ibises, roseate spoonbills, tanagers, orioles, grebes, terns, and ducks, and other waterfowl. As some of the more biologically vulnerable and highly sought species reached endangered status as the feather trade boomed, conservation groups in the United States (and elsewhere) began to organize educational campaigns. Eventually, public outcry against the destructive overexploitation of the beautiful, but rapidly vanishing bird species enhanced public awareness of their impending extinction and encouraged many fashion-conscious consumers to reduce or control their demand. Some protective laws were eventually passed; however, public action probably more than anything else helped to reduce excessive consumer demands, discourage the feather fashion craze in general, and gain support for needed conservation legislation—thus saving most of the threatened birds from the brink of extinction. As a result, nearly all of these once threatened species still exist, and although some are now threatened by other human activities, many have fully or nearly recovered and are no longer in danger of extinction.

In addition to the human-induced processes that contribute to the depletion or extermination of particular species which provide superior or unique sources of wildlife products (see Chapter 9), one must also consider the impact of the increasing rarity of such species on related taxa which yield alternative but inferior economic products. Perhaps the best example of this is the progressive elimination of crocodile and caiman species—reptiles harvested for their valuable hides. This trend parallels that observed previously for the progressive depletion of superior, and later inferior (smaller) species of edible oil-bearing whales (Chapter 3). In the South American crocodile skin trade, the first choices were the Orinoco (*Crocodylus intermedius*) and American (*C. acutus*) crocodiles, because these species lack the osteoderms (bony plates) on the belly skin which reduce the overall value of the hide. When these preferred species became scarce, hunters turned their attention to the "bonier" species—the black (*Melanosuchus niger*) and broad-snouted (*Caiman latirostris*) caimans. When these had become depleted as well, populations of the smaller and much bonier species, *Caiman crocodilus*, also began to be harvested for the small neck skin pieces which were useful. By 1975, four subspecies of this Latin American caiman were considered endangered, whereas only two subspecies were listed as such by the late 1960's. As the trend toward harvesting less preferred species gradually increased, specimens of the more economically desirable species were inevitably slaughtered each time they were encountered. Thus, by shifting from superior, but depleted resource species to inferior, but more common species, most such harvesting operations can be sustained, though often to the detriment of the dwindling populations of the superior resource species.

Finally, in addition to considering the biological impacts of overharvesting, the economic impacts can also be substantial if not disastrous for the industry involved. For example, the decline of crocodile tanning and manufacturing industries in the United States and other nations has resulted principally from overexploitation of wild populations, a process fueled by the excessive commercial demands for crocodile leather. Worldwide, at least 5-10 million hides were traded each year dur-

ing the 1950's and early 1960's. By 1965, exports from India, west Malaysia, Africa, South America, and other exporting regions had declined to insignificant levels in comparison with the productivity observed in previous decades, despite the widespread absence of regulations or prohibitions on harvesting. More than 20 crocodile tanneries and manufacturing firms were in operation in New York City in the 1950's. However, by the time that protective legislation had been passed and finally began to be instituted (mid-1970's), few sizeable populations of these great reptiles were left to conserve!

In the sections which follow, the various types of industries or economic activities commonly implicated in international trade in endangered or threatened wildlife species are covered in greater detail. It is important to note at the outset, however, that the relatively recent passage of protective legislation or treaties and their implementation and enforcement have been and can be very effective in promoting the conservation of economically valuable, but endangered wildlife species. This is particularly true for species being overharvested in order to meet high market demand-price situations. For example, the American alligator, once an endangered species, is now recovering as a result of protection; states such as Louisiana and Florida which have established programs to control harvests and monitor alligator populations were recently granted permits to allow the harvest and export of alligator hides for commercial purposes. The same observations can now be made for a number of other previously endangered taxa; and if CITES succeeds in regulating trade in threatened species, which it now promises to accomplish, perhaps most of the species noted as being endangered principally by the international wildlife trade will become known as species *previously* endangered by the trade. Thus, the discussions and tables which follow should be considered in this light. Additionally, the species examples listed in Tables 1-3 were chosen on the basis of the criterion that they have been or are principally threatened by the economic activity in question (as were the other examples provided in the following sections); yet nearly all of these species have also been adversely affected by habitat destruction and other human activities. Thus in most instances, the trade activities discussed have played the major role in the demise or decline of the species mentioned, but they have not usually been the sole cause of their endangered or threatened status.

The Fashion Industry and Endangered Species

Crocodiles and caimans are but one group of higher animals (vertebrates) represented by many species that have been threatened with extinction by certain sectors of the fashion industry. Table 1 provides a sample listing of some of the better known examples. With the exception of stockpiled items and sea turtles and their products, these wild species are no longer *legally* entering commercial trade, primarily as a result of the adoption of CITES by most of the major consumer nations in recent years.

Reptile Products. Ever since the passage of some protective legislation for regulating trade in crocodile hides, both illegal and legal slaughter (of individuals in unprotected but depleted populations) has continued on a large scale. For example, about 2 million crocodile hides were traded internationally in 1976. Even though some of this productivity was obtained from more common and unprotected species, a great proportion of the hides sold were claimed to have been legally caught, but were in

TABLE 1. Species Endangered Principally by the Fashion Industry

Common & Latin Names	Most Recent Geographic Distribution	Principal Products/ Other Causes of Decline
REPTILES:		
Hawksbill turtle *Eretmochelys imbricata*	Tropical oceans	Tortoiseshell for jewelry, hair combs, etc.; skins.
Olive or Pacific ridley turtle *Lepidochelys olivacea*	Indo-Pacific and Atlantic Oceans	Skins; also for edible oil and eggs.
Broad-nosed caiman *Caiman latirostris*	Southern Soutn America	Hides for novelty leather trade.
Black caiman *Melanosuchus niger*	Amazon basin (scattered)	Hides; recent habitat loss due to cattle ranching.
American crocodile *Crocodylus acutus*	United States; Mexico; Honduras; Venezuela	Hides; sport hunting; loss of habitat; human disturbance.
Orinoco crocodile *Crocodylus intermedius*	Venezuela	Hides.
Morelet's crocodile *Crocodylus moreletti*	Mexico; possibly Guatemala	Hides.
Marsh or swamp crocodile *Crocodylus palustris* (2 subspecies)	India; Iran; Pakistan; Sri Lanka	Hides; loss of habitat and food resources; also natural factors.
Saltwater crocodile *Crocodylus porosus*	Indo-Malaysia; Philippines; Indonesia	Hides (unsurpassed for leather).
Siamese crocodile *Crocodylus siamensis*	Thailand	Hides.
Dwarf crocodile *Osteolaemus tetraspis*	West Africa	Hides; meat and eggs also.
Indian gavial *Gavialis gangeticus*	India; Pakistan	Hides; habitat loss.
False gavial *Tomistoma schlegelii*	Malay peninsula; Borneo & Sumatra	Hides.
Indian/Burmese python *Python molurus*	India; Burma; S. China	Skins; used for food in Hong Kong; habitat loss and human disturbance.
Central Asian gray monitor *Varanus griseus caspius*	USSR: Iran; Pakistan; Afghanistan	Skins; also flesh; sport hunting; habitat loss.
BIRDS:		
Chinese Egret *Egretta eulophotes*	Korea; Hong Kong; China	Feathers (late 19th C.); after decline, competition from another egret species.

TABLE 1. (Continued)

Common & Latin Names	Most Recent Geographic Distribution	Principal Products/ Other Causes of Decline
Japanese Crested Ibis *Nipponia nippon*	Japan; Korea	Feathers (1870-90); hunted for meat; habitat destruction.
Short-tailed Albatross *Diomedea albatrus*	Torishima Island, Japan	Feathers (1887-1903).
MAMMALS:		
Chinchilla *Chinchilla laniger*	Andes—Bolivia & Chile	Fur.
Cameroon clawless otter *Aonyx microdon*	Cameroons; Nigeria	Fur.
Giant otter *Pteronura brasiliensis*	Amazon basin & drainage systems	Fur (as valuable as high-quality jaguar pelt).
La Plata otter *Lutra platensis*	S. Brazil; Paraguay; N. Argentina; Uruguay	Fur; water pollution.
Southern river otter *Lutra provocax*	Chile; Argentina; Andes	Fur; water pollution.
Southern sea otter *Enhydra lutris nereis*	Monterey, CA to Channel Islands, CA	Fur; recently, persecution from abalone fishermen.
Formosan clouded leopard *Neofilis nebulosa brachyurus*	Taiwan	Fur; captured for zoo specimens.
Snow leopard *Panthera uncia*	USSR; China; India; Pakistan; Afghanistan	Fur; hunted for sport; combatted as pest; loss of prey & habitat.
Tiger (6 subspecies) *Panthera tigris*	USSR: Afghanistan; Iran; Indonesia; China	Fur (especially Siberian & Bengal); persecuted as pests; loss of habitat & prey; hunted for sport and live trade; medicinal uses.
Asiatic cheetah *Acinonyx jubatus venaticus*	Turkmenistan, USSR, Afghanistan	Fur; persecuted by man; loss of habitat and prey.
Galapagos fur seal *Arctocephalus australis galapagoensis*	Galapagos Islands	Fur (1535-19th C.).
Juan Fernandez fur seal *A. philippi*	Juan Fernandez Archipelago	Fur (1683-1824).
Guadalupe fur seal *A. townsendi*	Guadalupe Island	Fur (nearly extinct by 20th C.).
Hawaiian monk seal *Monachus schauinslandi*	Hawaiian Islands	Fur (nearly extinct early 20th C.); also harvested for oil, disturbance by humans and dogs.
Vicuña *Lama vicugna*	S. America, Central Andes (plains)	Hide for fine wool; used for meat; competition with livestock.

Sources: IUCN *Red Data Book*, Vols. 1-3; Ziswiler, 1967.

fact hides from endangered or protected species. As a combined result of the actual biological scarcity of wild specimens, coupled with more stringent regulations on trafficking in hides and greater protection of some of the dwindling populations, fewer hides are now reaching the market than in the previous decades of excessive hunting. As a result, prices have skyrocketed in recent years. For example, Japanese imports of raw hides averaged about $14/kg ($6/lb) in 1970, but by 1978 had increased by more than 275 percent to $39/kg ($18/lb); similarly, imports of prepared crocodile leather cost roughly $29/kg ($13/lb) in 1970, but eight years later had increased by more than 525 percent to over $156/kg ($71/lb).

Along with the increased demand for reptile leathers and the depletion of wild crocodile populations worldwide, prices paid for both wild and farm grown American alligator (*Alligator mississippiensis*) (Fig. 3) have also increased. At a Louisiana auction in 1976, the average price paid per wild-harvested alligator skin was $117 ($53/m, or $17/ft). However, prices paid were lower at the 1977 auction—declining to an average of $89 per hide ($40/m, or $12/ft); the total amount paid for 5,275 hides (in addition to the slightly less valuable hides from 351 pen-raised animals) amounted to nearly $0.5 million in that year. Recent prices paid for finished products have been staggering. In early 1981, prices for western boots made from American alligator skin retailed for about $1,800 to $2,000 per pair in Texas, while crocodile skin boots cost up to $1,800. In 1978-1979, a single Nile crocodile handbag similarly ranged from $1,000 to $2,000. At such prices, it is no mystery why poaching of the more valuable but very endangered species continues. Moreover, up to 50 percent of the hides sold on the market may be commercially useless due to improper hide preservation in the field; thus, roughly half of these animals may be dying needlessly—probably about 1 million in 1976 alone.

Fig. 3. Once endangered, the American alligator has recovered due to formal protection during the late 1960's and early 1970's. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI)

Crocodiles, alligators, and caimans are merely one group of reptiles that are threatened by certain sectors within the fashion industry. Many species of lizards, snakes, and turtles are also threatened by the skin trade. As adequate supplies of crocodile and other preferred reptile skins began to decline, skins from anacondas, boas, pythons, monitor lizards, iguanas, cobras, and a great variety of other lizards and snakes began to enter the market. During the 1950's, as many as 12 million snakeskins were traded annually. In 1976, over 3 million snakeskins were exported by India and over 350,000 from Indonesia; the latter country also exported more than 270,000 iguana skins. For example, a retail outlet in London was selling around 10,000 lizard bags annually until 1978 when adequate supplies of the skins became difficult to obtain; each bag required the use of skins from 6 to 12 lizards. Reptiles are important natural predators, and extensive hunting and removal of significant numbers can produce ecologically unfortunate results. Snakes are particularly valuable for controlling rodent populations; when the snake processing industry was booming in India during the 1950's, rat infestations reached a peak in Madras due to the overkill of local snake populations. When the rat infestation reached its peak, 5,000-10,000 snakeskins were being processed daily at the Madras tannery.

Sea turtle leather has also figured more heavily in the world skin trade in recent years. Sea turtle leather was insignificant in international trade until the 1960's, when it began to be used as an economic substitute for dwindling supplies of crocodile skins. Mexico, the first nation to extensively exploit these reptiles, set up tanning industries based primarily on the olive ridley (*Lepidochelys olivacea*). Each year, new rookeries (breeding grounds) were exploited and destroyed until the two largest tanning firms ended their production in 1977, admitting that the brief, but lucrative trade had destroyed the resource base. Turtles are slaughtered for their front and hind flippers; each set sold for \$27 in 1976, whereas each was worth only \$1.50 little more than a decade before. By 1979, the average price of raw turtle skin ranged from \$4.87/kg (\$2.21/lb) to \$11.56/kg (\$5.24/lb). In 1977 and 1978, 150,000 live olive ridley sea turtles were captured for the skin trade in Mexico and Ecuador.

Sea turtles are also used for their edible eggs, oil, and meat; turtle oil is also used in making certain cosmetics and industrial products. However, probably the most notable sea turtle product is tortoiseshell—obtained principally from the hawksbill turtle (*Eretmochelys imbricata*). The shell from this species has been sought since ancient times for fashioning jewelry, hair pins, artwork, and souvenirs or crafts for the tourist trade. When the plastics industry became established during the 1930's and expanded rapidly, it appeared for a while that imitation tortoiseshell would relieve depleted hawksbill populations. However, the irreplaceable beauty of the natural product and, to a much lesser extent, the rapidly expanding market for turtle flippers (skins) and flesh (meat), eggs, and calipee as a substitute for these products from less abundant but more preferred turtle species, have all contributed to the renewed and expanding commercial interest in this species. Thus, the survival of this sea creature, and the tortoiseshell industry based upon it, is again in doubt. From 1976 to 1978, the equivalent of an average of several hundred thousand hawksbill turtles were traded annually for the tortoiseshell trade, primarily from the waters off Indonesia, Thailand, India, Fiji, and the Philippines. Currently all species of sea turtle are protected by CITES and importation of any type of sea turtle product into the United States is illegal.

Furs and Fleece. The large spotted (and striped) cats, many seals, and sea and river

otters have been especially valued for their fur, and hence many of them have become endangered because of the fur business. By the 1950's many of the spotted cats, particularly the snow leopard, clouded leopard, and cheetah, were already threatened by the fur trade. Despite signs of depletion, great numbers of spotted cats were continually harvested throughout the 1960's for export to the United States, Europe, Great Britain, and fashion centers in Paris and elsewhere. Prior to the imposition of U.S. import bans on products from endangered species, the United States imported $9.8 million worth of spotted cat hides in 1968 and nearly $10.6 million in 1969. The number of animals killed to meet 1968 demand alone were 1,300 cheetahs, 9,600 leopards, 13,500 jaguars, and 129,000 ocelots. The International Fur Trade Federation recommended a temporary 3-year ban on the cheetah and leopard and a voluntary trade ban on the clouded and snow leopards and tiger in 1971. Although this recommendation was heeded by the United States and other countries, many other nations did not comply; and by 1973 many of these species were clearly endangered. Prior to 1979, a number of producer and consumer nations had failed to sign or enforce CITES; until then, CITES was relatively ineffective in monitoring and regulating such international trade. Thus, by the 1970's only an estimated 500 snow leopards remained in the mountains of Asia and the Himalayas; the clouded leopard is similarly now very rare. The leopard of Africa and Asia, the most widely distributed of all the big cats, has become severely depleted throughout many parts of its range, as has the once very common jaguar of South America. The Bali and Caspian tigers are now considered extinct, and the Javan tiger is very near extinction; the other five subspecies of tigers have not fared well either. There are an estimated 800 Sumatran tigers, and only 150 Siberian tigers left in Korea, China, and the Soviet Union. Clearly, unless consumers of spotted or striped cat products become more enlightened about the consequences of their desires for fur fashions, most of the large cats will be extinct by the year 2000. As the economically preferred species have become increasing scarce (both biologically and economically) and protected, the smaller cats such as ocelot (Fig. 4), margay, bobcat (Fig. 5), and lynx have become more intensively sought. By 1976, an undamaged South American jaguar pelt sold for $140, and a good ocelot pelt for $40. Now within the United States, the Texas ocelot (*Felis pardalis albescens*) is endangered, while the entire species (*Felis pardalis*) is considered vulnerable to extinction. In 1975, a Canadian lynx pelt sold for about $150, but jumped to $290-340 by 1978. Finished products, of course, typically sell for much higher prices and therefore higher profits. As an example, in Munich, Germany in 1979, an ocelot coat (10 skins) cost as much as $40,000, while a good quality lynx coat (10 skins) recently sold for $8,000-10,000.

Many of the same observations regarding the cat furskin trade can also be made with respect to the sealing industry and the otter fur trade, both of which can claim responsibility for endangering a number of species. The sea otter of North America (*Enhydra lutris*) (Fig. 6) once provided the most beautiful and valuable fur known; it also once ranged from Baja California to the Japanese Islands, along the coasts and island shores of the North Pacific region. Trade in sea otter pelts began in the late 1700's on the Chinese frontier; the best pelts sold for about $15-50 between 1775 and 1780. By 1786, they reached $70-91 each for first grade pelts—a very high price in those days. However, prices fell during the early 1800's due to the great numbers of animals that were being slaughtered, and they remained relatively low ($15-40 for the

Fig. 4. The ocelot *(Felis pardalis),* an important North American fur-bearing species. (Photo: C.E. Most, U.S. Fish and Wildlife Service, USDI)

best pelts) until 1873 when the average price per pelt rose to \$75. By 1887, average prices reached \$100, with the best skins selling for \$350; after this date, the prices continued to climb. Otter populations in the Northern Pacific had already begun to show signs of serious depletion before this time; for example, the last 42 otters in San Francisco Bay were killed in 1847. Each year, fewer pelts entered the market during the late 1800's; and by 1903 average prices for good pelts were \$440, with large, extra rich pelts commanding prices as high as \$1,125 each. By 1910 the United States government extended protection to the few remaining otter populations, and only one pelt reached the London market that year; it sold for over \$1,700. Without formal protection by the U.S. government, it is likely that at such prices, commercial harvesting would have continued until the sea otter was virtually extinct everywhere. Since sea otters are predatory animals which play a major role in structuring and influencing the species diversity present in nearshore marine communities, their depletion or loss over wide areas has probably resulted in significant changes in the structure and functioning of Pacific coastal marine environments.

In addition to providing furs, wild animals are also sometimes used as a source of wool fibers. The most sought after and valuable fleece known—one far more valuable than that of the Persian lamb or karakul—is that of the vicuña (*Lama vicugna*). The vicuña is a shy, camel-like relative of the alpaca; both are from South

Fig. 5. The bobcat *(Lynx rufus)* and other small cats have been more intensively sought as the larger fur-bearing cat species have become scarce. (Photo: C.L. Cadieux, U.S. Fish and Wildlife Service)

Fig. 6. The sea otter *(Enhydra lutris)* once supported the lucrative U.S. otter pelt trade. Today only a few scattered populations of this marine mammal survive. (Photo: W.C. Loy, U.S. Fish and Wildlife Service, USDI)

America. The vicuña of the Andean plains are very fast runners; and they are extremely difficult to hold down for shearing; and they have been very difficult to domesticate. As a result, wild populations have been decimated for their valuable fleece, which cost around $55/kg ($25/lb) in the late 1960's. A single yard of vicuña cloth, however, may require the fleece of a dozen animals. Demand for vicuña cloth and for their pelts to make fashion coats and other apparel during the 1950's brought this species close to extinction. At the beginning of that decade, the total population was estimated between 100,000 and 400,000 individuals; but by the 1960's, only about 15,000 animals remained. Today this endangered species is recovering as a result of the establishment of wildlife reserves in Peru and heavy protection against poachers who, in the past, resorted to helicopters, machine guns, high-powered rifles, and water poisons to obtain the valuable pelts of these wary animals. The success of these current conservation efforts are fortunate, not only because of the irreplaceable uniqueness of this finest of all wool-producing animals; but also because of the value of this high-altitude adapted species as an animal research model for the study of blood transport of oxygen and body temperature regulation in extreme, high altitude environments. Moreover, if the vicuña recovers and can be effectively managed in a semidomesticated state, it may provide a valuable source of income for the Andean plains peoples, and thus provide a basis for enhancing the economic development of the Andean high plateau.

Tourist Curios and Other Collectors Items

Harvesting of wildlife for the production of souvenirs, ivory or other raw materials for production of artifacts and other collector's items also contributes to the depletion or extinction of species. The souvenir or curios trade accounts for some of the more bizarre and often wasteful uses of wildlife, e.g., elephant feet wastepaper baskets, elephant or gnu tails for fly swatters, and leopard or cheetah heads for trophies, even though in many cases these items are by-products obtained from harvesting or poaching of animals for other purposes. Some animals, however, are harvested directly to be stuffed or preserved for tourist souvenirs or items of trade. For example, stuffed birds of paradise sell for $215, and young sea turtles, crocodiles, and caimans are also preserved or stuffed (if they are not harvested for the pet trade) for sale to tourists. Gorillas, although principally threatened by habitat loss, are being increasingly poached for their heads and hands which fetch high prices as tourist curios, e.g., gorilla-hand ash trays. Considering the great value of all nonhuman primates for biomedical, psychological, and anthropological research, the indiscriminate slaughter of these harmless, intelligent animals is a great travesty.

Other popular collecting habits which threaten the existence of species include the demand for mollusc shells, butterflies, and artifacts fashioned from ivory or tortoiseshell. In 1978, the United States imported nearly $11 million worth of crude and worked marine shell pieces (4.3 million kg or 9.5 million lb), $0.5 million worth of crude coral (about 0.75 million kg or 1.67 million lb), almost $1 million worth of sponges (45,350 kg or 100,000 lb), and $7.4 million of raw and worked ivory (9,070 kg or nearly 20,000 lb). The shells of the giant marine clam (*Tridacna gigas*) are so large (113 kg or 250 lb) that they are frequently sold in the United States and Europe as wash basins. In a London shell shop in 1978, giant clam shells were selling for $80-480 per pair. However, exotic, beautiful marine shells are in the greatest demand

and consequently fetch the highest prices; these include the cowries, tritons, conches, helmet shells, and other colorful tropical species. Most of these are obtained from reefs and shore areas of Hawaii, the Philippines, East Africa, and Papua New Guinea. However, some shells are obtained on land. The green tre snail (*Papustyla*) *pulcherrima*) is fancied by collectors and is often used in jewelry pieces for its beautiful green color, while beautiful *Polymita* snail shells are collected in Cuba. Extensive collection of the latter species is contributing to the decline of the rare Cuban Hook-Billed Kite which depends primarily on *Polymita* snails for food.

Butterflies are also very popular with tourists and collectors. Collection of beautiful or unique butterflies supports cottage industries in some areas of Latin America, Asia, and Australasia. For example, the butterfly trade in Taiwan supports 20,000 people, about half of whom are collectors; in recent years about 20 million butterflies have been caught annually, and 1966 exports from Taiwan were valued at $30 million. In South America, great quantities of butterflies are harvested each year—in Brazil perhaps as many as 50 million annually. The wings are removed from most specimens and are used for decorating candles, making butterfly plaques, or replicas of well known art pieces (e.g., the "Blue Boy") and other artistic designs. Some of these butterfly "paintings" sell to tourists for hundreds of dollars. Other butterfly species are collected primarily for pressed specimens for sale to butterfly enthusiasts worldwide. Japan is the primary importer; however, the United States and many European countries are also major importers. One dealer in England displayed $300,000 worth of Papua New Guinea butterflies for sale in 1976. Some advertisements in the United Kingdom have proposed the purchase of rare and beautiful butterflies as a hedge against inflation; in 1969 one birdwing butterfly sold for $1,875! And a pair (male and female) of rare Rothschild's birdwing butterflies were priced at $850 in Japan.

Unfortunately, excessive harvesting, coupled with the destruction of their forest habitats, is depleting many such tropical forest populations. In particular, the birdwings, members of the swallowtail family which reside in Australasia and Southeast Asia, include the largest and some of the most beautiful butterflies in the world. The males reach the largest sizes; for example, a male Queen Alexandra's birdwing (*Ornithoptera alexandrae*) typically has a wingspan of 20 cm (8 in). The Queen Alexandra's and paradise (*O. paradisea*) birdwings are two of the most prized collector's items in the world. These and other unique and rare birdwings command export prices of $200-1,200 per pair, and demand is already outstripping available supplies. The most prized birdwings exist only in isolated areas of New Guinea and some of its neighboring islands. They specialize in feeding on *Aristolochia* species, plants which typically contain poisonous or toxic compounds; some species are employed in the Americas as medicinal herbs for treating snakebite and convulsions. Some of the rarer birdwings are in danger of extinction; the threatened species represent most of the few well-documented examples of overcollecting as a threat to the survival of insect species. Although most insect species have great reproductive potential in comparison with higher animals, most giant birdwings do not. Now that populations of some of the more valuable species are depleted, greater attention is being paid to raising them on "butterfly ranches," small areas planted with their larval host plants (aristolochias) and their favorite adult nectar plants. Some birdwing ranches have already been established in Papua New Guinea, and they are producing superior specimens for collectors while simultaneously helping to reduce harvesting pressures

on the wild populations. Most of the butterflies valued as collector's items are threatened by tropical deforestation and disturbance of secondary growth habitats associated with these ecosystems. As their forest habitats, and therefore their food and nectar resources, continue to disappear, "ranching" may be the only conservation strategy which will effect the survival of some of these valuable species as well as other insects, e.g., the large stag beetles, which are also prized as collectors' items.

The great demand and consequent value of ivory for scrimshaw, jewelry and jewelry boxes, and other collectors' items has threatened the existence of Atlantic and Pacific walruses (*Odobenus rosmarus*) and the African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants. The latter two species are also hunted for sport, used for food and their skins, and have suffered from loss of habitat, while the penis bone ("oosik") of male walruses is sold as a tourist curio in Alaska. Ivory has been used as a medium for carving and production of artifacts since paleolithic times, and it has been used for such purposes in most urban cultures throughout history. In recent times, however, ivory has been collected and hoarded as a guarantee against inflation. In times of monetary instability, highly durable ivory tusks and art pieces are sometimes valued more than gems, paintings, and valuable antiques. Thus, raw ivory prices have steadily increased. The wholesale value of raw walrus ivory climbed to $55/kg ($25/lb) by 1981, and raw elephant ivory has risen from about $6/kg ($2.75/lb) in the 1920's, to $7-22/kg ($3-10/lb) in the 1960's, and $110/kg ($50/lb) in the 1970's. Walrus populations in Alaska are formally protected under the Marine Mammal Protection Act of 1972. Yet, the number of animals killed annually in Alaska increased from 1,500 animals in 1979 to an estimated 5,000-6,000 in 1980. The kill figure for 1981 is projected to top 10,000 animals, indicating that the lack of restrictions on walrus hunting by Alaskan natives for purportedly "nonwasteful subsistence purposes" must be reevaluated. Although the African elephant is a threatened but not yet an endangered species, recent high prices for ivory have encouraged both legal and illegal trade; in 1972, Kenya's exports alone were 150 metric tons. In 1973-1974, elephant killing reached an all-time peak, and the glut of ivory on the market resulted in a decrease in prices to $55/kg ($25/lb). Despite this decline, the great value of ivory still provides a strong incentive for the slaughter of elephants; in 1976 consuming nations imported more than 1.25 million kg (2.75 million lb) of raw ivory from an estimated 72,300 elephants, and nearly 1 million kg (2.2 million lb) in 1977 from about 56,200 elephants. Discrepancies between import and official export figures indicate that nearly 0.5 million kg (1.1 million lb) of the 1976 and 1977 production was obtained from more than 26,500 poached animals; poaching is believed to be most severe in Kenya and northern Tanzania.

Roughly 1.5-3.0 percent of these raw ivory exports entered the United States. Worked ivory pieces, including beads and artwork, have been imported by the United States as well, primarily from Hong Kong, Japan, and China. The total import value of these worked ivory pieces amounted to more than $4.6 million in 1977, over $7 million in 1978, and about $2 million during the first half of 1979; the estimated weight of these pieces (from 1977 to May 1979) was from 82,000 to almost 150,000 kg (180,800-330,750 lb)—or from 4,700 to 8,500 elephants. Clearly, given the demand for and value of ivory, this trade must be regulated, and severely depleted elephant (or walrus) populations and their natural habitats must be more fully

protected if a sustainable yield of raw ivory is to be maintained in the coming decades. Failure to do so will result in extinction of the African elephant and other ivory-bearing species.

The Live Animal Trade

The collection of animals from the wild for pets, zoo specimens, and research institutions is a trade of significant volume. In comparison with trade in wildlife products *per se*—where for every animal sold alive, 100-1,000 specimens are sacrificed for hides, furs, feathers, meat, or other products—it may seem insignificant. However, it is important to note that the live trade involves the extraction and use of very different wildlife species, and encourages the depletion or extinction of a much broader range of biological resources. At least 5.5 million wild birds and several hundred million (up to a billion) fish, reptiles, and amphibians are traded internationally each year. Worldwide, the cage bird and turtle trades are each multimillion dollar businesses; similar conclusions can be drawn with respect to the wholesale (or retail) value of trade based on the other major groups of wildlife which enter the live trade. For example, in 1978 the U.S. retail cage bird industry was valued at more than $178 million, with roughly $100 million accruing from the sale of wild birds alone, while live birds imported into the United States in that year (for wholesalers) amounted to a declared value of nearly $8 million. Over a 9-month period from 1979-1980, more than 442,000 live birds entered the United States; nearly half were psittacines (parrots, parakeets, macaws, lories, including individual animals representing 40% of all known parrot species). In 1980, more than 400,000 live reptiles, mostly species of small size for the pet trade, also entered the country. Similarly, in 1978 the United States imported more than 260 million tropical fish primarily for the ornamental aquarium trade; in 1978 such imports were valued at more than $17 million (declared import values). The wholesale value of exotic fish raised on Florida fish farms has topped $30 million annually in recent years, and the industry supports thousands of people. Morevoer, at least 20 million U.S. homes have aquaria, and the annual retail sales of only the three largest suppliers of exotic fish amounted to approximately $350 million in 1971. Yet even though the live animal trade is lucrative, importation of exotic wildlife is, in many ways, a costly and hazardous venture. Part of the trade involves rare or endangered species, many of which are strictly protected within their country of origin; and the pet trade, in particular, is a major threat to the survival of a great number of endangered birds, reptiles, and amphibians. In addition, exotic plant and animal wildlife can pose threats to human health, and they frequently become established in new environments, causing major economic and ecological problems and endangering native plants and animals.

Exotic fauna sometimes threaten human health and even human life, e.g., a pet python, which was probably underfed, recently killed and attempted to consume a sleeping infant in Dallas, Texas. Tigers and other large cats kept as pets have been known to attack their owners, and emergency personnel called out to retrieve abandoned pet alligators or crocodiles from swimming pools or waterways are often bitten. It is likely that no one wants to contemplate the threats that venomous cobras or piranha fish might pose to human life or health; yet two Asian cobras were captured live near Miami, Florida, and at least two released white piranhas managed to survive the fourth coldest winter recorded in Florida's history. We can also contract ex-

otic diseases from introduced wild animals. Parrot fever (psittacosis) can be contracted from wild birds; in humans it causes a pneumonialike infection and a high fever. Turtles can carry dangerous forms of *Salmonella*, including *S. enteritidis*, *S. typhi* and *S. typhimurium*, and salmonellosis can be transmitted from pet turtles to humans. Prior to the imposition and enforcement of import bans on exotic turtles entering the pet trade, an estimated 280,000 cases of salmonellosis were believed to be linked to pet turtles each year; most of these infections occurred in children.

Exotic diseases transmitted by introduced wildlife also pose a threat to domestic animals, and sometimes such disease epidemics produce substantial economic losses. For example, cage birds imported for the pet trade often carry exotic Newcastle disease (VVND), a highly contagious disease that is usually fatal to domestic fowl and for which a truly effective vaccination does not yet exist. Although many wild birds carry VVND, they are usually not affected by it until they become stressed or ill for other reasons. The overcrowded conditions characteristic of most wildlife transport operations are frequently traumatic enough to cause outbreaks of VVND in quarantine stations or in pet shops—particularly those which obtain their birds illegally. Sometimes these localized epidemics spread, and eventually infect domestic fowl and native birds. During 1971 and 1972, serious outbreaks of VVND occurred in California and New Mexico, and the USDA was forced to destroy approximately 12 million chickens and other poultry (Fig. 7). The cost to U.S. taxpayers was $56 million—a heavy price to pay to support a trade in exotic cage birds, especially when considered on top of our expenses to support the USDA quarantine facilities, in part for import dealers.

Fig. 7. Wherever a VVND outbreak occurs, appraisers count the chickens or other affected poultry before destroying them; the owner is later indemnified for his loss by the U.S. government—a cost that is passed on to taxpayers. (Photo: USDA)

Exotic species are often released into new environments within consumer nations by persons who tire of their pets as well as by accidental escape from special, commercial propagation areas. Such accidental or intentional introductions may have a variety of economic and ecological consequences. Some exotic mammals compete with livestock for rangeland resources, while others prey on valuable gamebirds or on beneficial native species. For example, the Cuban tree frog, introduced into Florida, preys on native tree frogs which have been important predators of citrus tree insect pests. The introduced, giant poisonous toad (*Bufo marinus*), source of the compound marinobufagin which has interesting cardiac and anticancer properties, even competes with household pets for their food. If a wary dog moves to defend its food bowl, it contacts a poisonous secretion when it seizes the sluggish animals. Although many dogs have not survived, those that do quickly learn to leave the giant toads alone to feed in peace.

Displacement of native flora and fauna is probably the most unfortunate consequence of the introduction of nonnative wildlife to new environments. For example, consider the role of the booming ornamental fish industry in Florida in displacing a number of native fish species. By 1970, more than 250 fish farms were in operation in Florida, and they supplied nearly 80 percent of the U.S. demand for aquarium fish. But, these fish farms lacked effective safeguards to prevent the escape of exotic fish into connecting waterways or open waters; as a result, between 1968 and 1972, 38 exotic fish species and many of their hybrids became well-established in Florida waters. Many of these species are aggressive, territorial competitors or voracious predators which interfere with or consume native fishes and other aquatic wildlife species. Some of them carry exotic diseases which can decimate previously unexposed native fish. As a result of such accidental introductions, many beneficial species, such as the mosquito-eating *Gambusia*, have declined, and some native fishes are now endangered. Exotics such as the black acara (*Cichlasoma bimaculatum*) and the albino form of the walking catfish (*Clarias batrachus*) now have very extensive ranges in southeastern Florida. In one canal near the suspected site of initial introduction, black acaras now account for 80 percent of the total fish biomass. Walking catfish, which expand their range during rainy seasons by "walking" (flip-flopping) to new ponds or other aquatic environments, feed avariciously on plants, insects, and other fish. They are also capable, however, of living for up to 8 months without food!

In addition to threats to human health, to socioeconomic considerations, and to displacement of native biota by nonnative wildlife, one must add the biological and economic consequences of losses of the species or populations that are being actively traded.

The Bird Trade. In recent years 75–86 percent of the birds imported to the United States have been wild animals. Trade in wild birds, as in the case of marine fish, has become highly lucrative; demand for cage birds in the United States and other developed nations has increased rapidly during the last decade, while supplies have steadily decreased since 1971. As a result, prices for many species, particularly the rare, unusual, or protected species, have skyrocketed. For example, endangered Little Blue (Spix's) or Indigo (Lear's) Macaws recently sold for at least $10,000 each. The Hyacinth Macaw (*Anodorhynchus hyacinthinus*), one of the most valuable but not one of the most threatened macaws, sold for $550 in Miami in 1971; but by 1979, individuals sold for $1,500-8,000, with one advertisement asking $25,000 for a pair. Although most Hyacinth Macaws exported from South America in recent years have

been shipped from Paraguay (where they do not occur naturally) or Bolivia (where only peripheral populations exist), it is believed that most of these have been illegally smuggled out of Brazil (where they are formally protected). Similarly, the Golden-shouldered Parrot (*Psephotus c. chrysopterygius*) is in such great demand that birds are regularly smuggled out of their native Australian habitat; since the current price of a single bird ($10,000) is several times that of the maximum possible fine ($3,000), smugglers find that the potential gains far outweigh the potential losses. Table 2 lists some bird species currently endangered or extinct as a result of the live trade; most individuals of these species are destined for the pet trade. Moreover, most of them are obtained from tropical forests or savannas, and most have formal protection over at least part of their range. Despite such protection, the outrageous prices that some aviculturalists are willing to pay might eventually bring about the demise of most of these species. Major import dealers are usually willing to special order a specimen of any species desired by the consumer—the only admonition the potential buyer may receive is that it will take more time to obtain an individual specimen of an endangered or rare species.

The live animal trade is generally very wasteful of the wildlife species which support the industry; however, the profit margins have typically been so great that the tremendous waste involved thus far has easily been compensated. As many as 100 million wild birds are traded annually, but only a fraction of these survive their first year of captivity. For every 1 or 2 birds which survive their journey, 5 die during capture and transport; the more delicate species typically suffer death rates (in transport) in excess of 80 percent. Even given the best conditions for transport and subsequent captivity, death rates are seldom lower than 40 percent for any one species. Using favorable figures, of the 75,000 Mynah birds (*Gracula religiosa*) believed to have been exported annually from Bangkok prior to 1977, an estimated 125,000 were actually removed from the wild. Moreover, since mynahs, many parrots, and other species nest in holes or cavities in trees, and since the natives often cut down the trees to obtain the nestlings for export, the harvesting process further contributes to the decline of such species by destroying potential future nest sites. Of the birds that survive the trauma of transport, many begin to exhibit stress-induced diseases; most animals are shipped without food or water (for days), in crowded, filthy cages. When Newcastle disease or other infectious diseases break out in quarantine stations, the diseased birds must be euthanized or returned to their country of origin. In 1976, quarantine station owners euthanized 14,790 birds which had VVND, while 15,353 birds died of the disease while at the quarantine station. A total of 51,314 birds were returned, but the majority of those probably did not survive the trip home. Analogous figures for 1981 were 21,182 (3 percent) euthanized and 83,778 (13%) died in quarantine. The total declared value of all live cage birds imported into the United States was $8.2 million in 1980 and more than $11.5 million in 1981.

The tremendous wastage of animal life caused by the cage-bird trade is deplorable, not only considering the statistics involved, but also the number of endangered species being traded. Many of these have important ecological or alternative economic uses in their native areas, and most of the threatened species reside within the resource-poor developing nations. The income received by natives for their harvesting efforts is often minimal and frequently makes it scarcely worth their while; for example, in 1977 native harvesters (collectors) received $0.60-1.00 per Mynah bird, while wholesale dealers in their country received about $30. In contrast,

retail prices in the United States at that time were approximately $350 per Mynah. Finally, nontarget species often suffer from the collecting operations as well. Aside from the obvious impact of habitat alterations, i.e., cutting down trees which serve as nest sites or food resources, birds of lesser or no trade value are caught and left to die in containers when the wholesaler refuses to purchase them. They are not released in order to prevent them from flying into the catching nets (mist nets) again.

Trade in Reptiles and Amphibians. "Snake rustling" and "turtle traffic" are two terms that are likely to be heard increasingly in the years to come, for high prices are also being paid for rare or unusual reptiles. In 1977, as much as $1 million worth of live tortoises, snakes, and lizards were being extracted annually from Arizona alone. Animal dealers listed prices then at $100-150 for a ridge-nosed rattlesnake (*Crotalus willardi*), $25 per Sonoran green toad (*Bufo retiformis*), and $150-300 for one gila monster (*Heloderma suspectum*)—all protected species which have been seriously depleted throughout their range and are now threatened with extinction. More common rattlesnakes ranged in price from $10-100, and a common desert gecko for only $2.50. Thus, as usual, the more rare the species, the more fashionable it is to own a specimen, and therefore the higher the price the consumer is willing to pay. Endangered eastern indigo snakes (*Drymarchon corais couperi*) have recently retailed for $185-250 each in northern markets. The distribution of this docile and attractive snake once extended from southeastern South Carolina west to the Mississippi River and south to Florida. Today, however, it is common only in southwestern Florida, where an active black market operation is centered on the collection and export of indigo snakes by trucks, cars, and commercial airlines. These and other species threatened by the live animal trade are listed in Table 3.

Worldwide, a great variety of reptiles and amphibians are collected, both legally and illegally, for the live trade. In 1970, the United States imported more than 1 million frogs and toads, over 70,000 salamanders, nearly 1.4 million turtles and tortoises, more than 200,000 lizards, about 110,000 crocodiles, and almost 32,500 snakes—about 2.8 million animals in all. The most commonly imported species included more than 880,000 leopard frogs (*Rana pipiens*), animals used for training students in the biomedical sciences; the giant marine toad, now an introduced pest in Florida; more than 1.8 million red-eared turtles, common children's pets; and iguanas, boa constrictors, and the common caiman—all of which are also valued for their hides or skins.

Just as in the case of the cage-bird trade, trade in live reptiles and amphibians is typically very wasteful and destructive of natural populations. From 5-10 million tortoises are believed to have entered international trade from 1965-1976, yet as few as 30-40 percent survive transport. For some species, only 1 percent of the animals survive their first year of captivity.

The Plant Trade

Many beautiful or unique plants which are potentially valuable as ornamentals or are used for such purposes are threatened by development projects and other forms of land conversion which irreversibly destroy their essential habitats. One example is the lovely persistent trillium (*Trillium persistens*) of Georgia and South Carolina. Other examples include many of the tropical irises, e.g., *Trimezia* and *Ti-*

gridia spp., and beautiful orchids of Latin America and West Africa. Development has even destroyed important vanilla orchid (*Vanilla planifolia*) habitats. The vanilla orchid is a climbing vine which inhabits wet, lowland rain forests in Central America. The town of Papantla, once a major vanilla-producing center in Mexico, is now devoid of both cultivated and wild stands of vanilla; and most vanilla now comes from Madagascar. A great number of other bizarre or beautiful plants, however, are threatened primarily from overcollection, principally many species of cacti (Cactaceae), lilies (Liliaceae), irises (Iridaceae), orchids (Orchidaceae), and some species of pitcher plants (Sarraceniaceae). For example, annual U.S. imports of orchids increased by more than 700 percent between 1960 and 1975, and the number of exporting nations has doubled during the last decade. However, since then U.S. orchid imports have declined from more than 400 million to about 175 million in 1981.

Naturally rare plants usually command the highest prices in catalogs of commercial dealers who deal in rare plants. Once commercial demand for an unprotected, rare species has become established, a never-ending spiral of demand-supply activities occurs until the species becomes endangered or extinct (Fig. 2). As a result of commercial demand and private collecting of rare, unusual, or useful plants, many species have become endangered in the United States within the last few decades. The Chapman rhododendron (*Rhododendron chapmanii*) from the pinelands of Florida is threatened from commercial exploitation; and in the southeastern United States, many species of carnivorous plants in pine forest stands are being depleted from overharvesting as well as being affected by monocultural forestry practices and urban-residential development. Pitcher plants are especially valued by florists and plant collectors. One plant dealer recently decimated one of the major populations of the green pitcher plant (*Sarracenia oreophila*), effectively eliminating 25 percent of all known stands during his raid at a state park in Alabama. Similarly, in a swamp area of North Carolina, butterworts (*Pinguicula*) and Venus' flytraps (*Dionaea muscipula*) are being overcollected.

In the southwestern United States, as many as 10 species and 10 distinct varieties of cory and pincushion cacti (*Coryphanthus* spp. and *Pediocactus* spp.), and two species and eight varieties of hedgehog cacti (*Echinocereus* spp.) (Fig. 8) are now considered endangered or threatened in the United States. Yet only a fraction of these and other commercially or privately overcollected taxa have been formally listed for protection under the Endangered Species Act of 1973. Other cacti which were once very common are becoming scarce, or they are being depleted at a very rapid rate. On an international scale, blackmarket trade in illegally harvested cacti from the southwestern U.S. and Mexico is estimated to be a multimillion dollar business. In the late 1970's, large Arizona barrel cacti (*Ferocactus; Echinocactus*) commanded prices of up to $350 each in New York City; one variety of *Echinocactus horizonthalonius* in Arizona is currently endangered by overcollecting, urban development, and destruction by off-road vehicles. Even the relatively common, tree-like saguaro cacti, *Carnegiea* (= *Cereus*) *gigantea*, which cover much of southwestern Arizona have become depleted in areas adjacent to some major cities due to their landscaping value for semi-arid urban and residential environments. Saguaros which sold for about $33-40/m ($10-12/ft) in the early 1970's were selling for at least $60-66/m ($18-20/ft) in the late 1970's (Fig. 10), while large, crested specimens have reputedly sold for as much as $1,000 each. Although Arizona has

TABLE 2. Birds Endangered Principally by the Live Animal Trade

Common & Latin Names	Most Recent Geographic Distribution	Principal Uses/Other Causes of Decline
Falcons & Allies:		
Philippine Eagle *Pithecophaga jefferyi*	Philippines	Captured for zoos & private collectors; stuffed for trophies; habitat loss.
Pheasants:		
Mikado Pheasant *Syrmaticus mikado*	Taiwan	Live animal trade; stuffed for curios; hunted for food.
Parrots & Allies:		
St. Vincent Amazon *Amazona guildingii*	St. Vincent Island, West Indies	Cage-bird trade.
Culebra Island Amazon *Amazona vittata gracileps*	Culebra Island	Live animal trade; habitat losses. Extinct (19th C.).
Glaucous Macaw *Anodorhynchus glaucus*	Paraguay; Uruguay; Argentina; Brazil	Cage-bird trade; possibly also for food.
Lear's (Indigo) Macaw *Anodorhynchus leari*	Bahia, Brazil	Cage-bird trade.
Caninde Macaw *Ara caninde*	S.E. Bolivia & N. Argentina	Cage-bird trade.
Red-fronted Macaw *Ara rubrogenys*	Bolivia	Cage-bird trade; hunted for feathers & food.
Cuban Red Macaw *Ara tricolor*	Cuba	Live animal trade; combatted as an alleged pest. Extinct (19th C.).
Spix's (Little Blue) Macaw *Cyanopsitta spixii*	East central Brazil	Cage-bird trade.
Thick-billed Parrot *Rhynchopsitta pachyrhyncha terrisi*	N.E. Mexico	Cage-bird trade; shot for food; habitat losses (logging).
Golden Parakeet *Aratinga guarouba*	N. Brazil	Cage-bird trade; recently, forest destruction.
Uvea Horned Parakeet *Eunymphicus cornutus uvaeensis*	Uvea, Loyalty Islands	Cage-bird trade; habitat losses (due to fire).
Scarlet-chested Parakeet *Neophema splendida*	Australia (interior)	Cage-bird trade.
Golden-shouldered Parakeet *Psephotus chrysopterygius chrysopterygius*	Queensland, Australia	Cage-bird trade; price is many times more than fine ($3,000).

TABLE 2. (Continued)

Common & Latin Names	Most Recent Geographic Distribution	Principal Uses/Other Causes of Decline
Hooded Parrot *Psephotus chrysopterygius dissimilis*	Northern Territory, Australia	Cage-bird trade (high prices).
Paradise Parrot *Psephotus pulcherrimus*	New S. Wales, Australia	Cage-bird trade; habitat loss. (Possibly extinct).
Trogons:		
Resplendent Quetzal *Pharomachrus mocinno* (2 subspecies)	Central America (scattered)	Cage-bird trade; habitat loss (coffee plantations, cattle grazing; subsistence agriculture).
Toucans & Allies:		
Toucan Barbet *Semnornis ramphastinus*	N.W. South America	Cage-bird trade; some habitat loss.
Sparrows & Allies:		
Long-wattled Umbrellabird *Cephalopterus penduliger*	N.W. South America	Cage-bird trade; hunted for food; habitat loss.
Marcgrave's Bearded Bellbird *Procnias averano averano*	N. Brazil	Cage-bird trade; forest destruction.
Rothschild's Mynah *Leucopsar rothschildi*	Bali	Cage-bird trade; forest destruction (human settlement).
Yellow-headed Picathartes *Picathartes gymnocephalus*	West Africa	Collected for zoo specimens & private collectors.
Red-headed Picathartes *Picathartes oreas*	West Africa	Cage-bird & zoo trade.
Seven-colored Tanager *Tangara fastuosa*	E. Brazil	Cage-bird trade; forest destruction.
Red Siskin *Carduelis cucullata*	N. South America	Cage-bird trade (esp. for hybridization with domestic canary).

Sources: IUCN *Red Data Book,* Vol. 2, *Aves,* 1978-1979; Nilsson and Mack, 1980; Ziswiler, 1967.

TABLE 3. Amphibians and Reptiles Endangered Principally by the Live Animal Trade

Common & Latin Names	Most Recent Geographic Distribution	Principal Uses/Other Causes of Decline
AMPHIBIANS:		
Frogs & Toads:		
Sonoran green toad *Bufo retiformis*	S.W. Arizona to W. Cent. Mexico	Overcollecting.
Goliath frog *Conrana goliath*	Cameroon; equatorial Guinea	Live animal trade; habitat disturbances & losses; killed for food.
REPTILES:		
Turtles & Tortoises:		
S. Amer. red-lined turtle *Pseudemys o. callirostris*	N. South America	Pet trade: stuffed for tourist souvenirs; used for food.
Argentine land tortoise *Geochelone chilensis*	Argentina; Paraguay	Live animal trade.
Desert/Gopher tortoises *Gopherus polyphemus* (2 subspecies)	S.W. U.S.—Texas; Northern Mexico	Pet trade; in U.S.—habitat loss, esp. due to off-road vehicles; in Mexico—used for food.
Pancake tortoise *Malacochersus tornieri*	Kenya to Tanzania	Pet trade; zoo specimens.
Madagascar spider tortoise *Pyxis arachnoides*	S. Madagascar	Pet trade; habitat destruction.
Spur-thighed tortoise *Testudo graeca graeca*	S.W. Europe to N. Africa	Pet trade; shells made into banjo curios for tourists.
Iguanas & Lizards:		
Ground iguana *Cyclura baeolopha & C. rileyi* (2 subspecies)	Bahamas Islands	Live animal trade; used for food; habitat loss; *C. baeolopha*—introduced predators.
Snakes:		
Aruba Island rattlesnake *Crotalus unicolor*	Aruba Island, off Venezuela	Live animal trade; habitat losses.
Ridge-nosed rattlesnake *Crotalus willardi*	S.E. Arizona, S.W. New Mexico; N. Mexico	Private collectors & collection for zoo specimens.
Eastern indigo snake *Drymarchon c. couperi*	S.W. Florida; rare throughout S.E. U.S.	Pet trade; habitat losses; harmed during rattlesnake collecting.
Jamaica boa *Epicrates subflavus*	Jamaica; Goat Island	Pet trade; introduced predators (feral cats, mongoose).
Two-striped garter snake *Thamnophis elegans hammondi*	California to Baja California	Pet trade; affected by pesticides and development.
Armenian viper *Vipera xanthina raddei*	USSR; Turkey	Pet trade; habitat losses.

Source: IUCN *Red Data Book,* Vol. 3, *Amphibia & Reptilia,* 1975.

Fig. 8. Known populations of the black lace cactus *(Echinocereus reichenbachii* var. *alberti* = *E. melanocentrus)* have been reduced by half due to overcollecting and brush clearing operations in its native Texas habitat. (Photo: D. Weniger, U.S. Fish and Wildlife Service, USDI)

passed strict laws to deter illegal poaching, the harvesting continues. "Cactus rustling" has become every bit as profitable as cattle rustling was in years past. Several dealers in Texas and other parts of the southwest pay illegal aliens one or a few cents for each small, globular cactus they can locate; the cacti are then sold on a massive scale from road-side stands or in urban areas for a few cents to a few dollars per plant.

In the Old World, trade centers on African succulents and Asian orchids. Although many of these species are propagated or grown from seed, a significant proportion of the trade involves wild-harvested plants; moreover, excessive seed collecting from wild populations may be adversely affecting the population densities of some species, such as *Pachypodium*, an unusual Old World succulent. Good specimens of wild-collected orchids from Indonesia fetch $11 each, and are being traded in increasing quantities. However, specimens of very rare orchid species may sell for up to $7,000 each. Tourists and private collectors, in addition to commercial plant harvesters, also contribute to the decimation of ornamental plant populations. One "cactus study" group of tourists from Germany uprooted an entire population of a rare *Mammillaria* species in Mexico in 1978; the tourists apparently purchased 15 suitcases in order to transport the specimens back to their country. The 1979 "cactus study tour" attempted to return 3,600 specimens of Mexican cacti to Germany. However, the plunder was seized at the Frankfurt airport and a court case was instituted against the offenders, a case which demonstrates the value of properly enforced international wildlife protection treaties such as CITIES.

Fig. 9. A saguaro cactus 4 m (12-14 ft) tall (*Carnegiea* = *Cereus gigantea*) for sale as an ornamental plant in Tucson, Arizona. (Photo: M.L. Oldfield)

It is evident that along with the prosperity increasingly enjoyed by many people in the industrialized nations, there has been an increased demand for horticultural plant specimens and an upsurge in interest in nonessential plant-collecting. If plant-collectors were only more aware of the impact of their desires and demands on rare populations, and if the trade could only be more effectively regulated and commercial species propagated to a greater extent, beautiful and unusual species could provide renewable resources for the live plant trade. However, very little progress is being made in this direction, just as in the case of the live animal trade. Since more common species can be harvested as rarer ones become endangered or extinct, such destructive ''business'' activities can undoubtedly continue into the far future, claiming even more species. However, very few people stand to gain from such practices, and everyone—especially future generations—will suffer from the accelerating loss of these ornamental or ''pet plant'' species. This is particularly true when one considers their known or unexplored potential for edible, medicinal, or other useful socioeconomic applications in human societies.

Fig. 10. Pyrethrum daisy flowers, source of pyrethrum insecticides. (Photo: Mitchell, USDA)

Miscellaneous Uses of Wild Biota

Plants also provide sources of other products used in industrial processes, or raw materials which support entire industries, e.g., fibers, spices and flavorings, essential oils, tannins, resins, dyes, and pesticides. Their uses for these industrial purposes are so numerous and varied that a detailed treatment cannot be provided here; however, some of the more important contributions of wild species to the production of these commodities should be mentioned.

Just as in the case of our cultivated agricultural and industrial crops, wild and weedy gene resources support our major fiber-producing crop species, and hence form the biological foundation of the textile industry. For example, fiber crops such as cotton (*Gossypium* spp.) and flax (*Linum usitatissimum*) clothe much of the world's population; demand for these fibers will probably increase as the cost of the petroleum-based synthetic textiles continues to rise. Other fiber-producing plants, such as jute (*Corchorus* spp.), hemp (*Cannabis sativa*), sisal hemp (*Agave sisalana*), and ramie (*Boehmeria nivea*) are used principally for the manufacture of lower-quality textiles, rope, twine, canvas, cordage fibers, and brooms and other household items. Of course, wild plant species related to these crop plants are used as sources of germplasm for genetic improvement purposes, as in the case of our food crop plants. Similar conclusions can be drawn for the major fiber-producing livestock species, particularly sheep. Silk fiber is obtained from the cocoons of either domesticated or wild silkworm moth larvae. The Far Eastern silk industry utilizes the cocoon silk of domesticated *Bombyx mori* silkworm larvae, which feed on the leaves of black and

white mulberries (*Morus* spp.). On the other hand, the Chinese and Indian tasar silk industries are based on the use of wild *Antheraea* silkworm species which feed primarily on wild but economically useful timber trees—including oaks (*Quercus*), meranti (*Shorea*), and Indian laurel (*Terminalia tomentosa*). Presently, forest sericulture of tasar silkworm larvae employs over 100,000 tribal families in tropical India, and it promises employment for nearly 1 million people in temperate areas; moreover, tasar silk exports from India, the world's second largest producer, amounted to $4.4 million in 1973.

Another wild animal species that yields an important industrial product is the lac insect (*Laccifer* spp.) which is used for production of shellac, a thermoplastic molding material and resin used as a polish base and source of varnishes. Natives encourage these insects to live on the twigs and young branches of fig and acacia trees in India and Southeast Asia. Most of our common household spices and many essential oils (for perfumes, flavorings, incense, etc.) are still obtained from tropical plants, while in contrast, most industrial flavorings, dyes and even tannins, are now obtained synthetically or semisynthetically. However, many such synthetics were modeled after the structural properties of the naturally derived chemical compounds. The study of natural pesticide compounds, for example, the study of physostigmine, a medicinally useful alkaloid obtained from the poisonous calabar bean (*Physostigma venenosum*) of tropical West Africa, led to the synthesis of novel methyl carbamate insecticides. On the other hand, other toxic chemical compounds with insecticidal properties are still extracted from plants for the manufacture of pesticidal products. The United States and other industrialized nations import hundreds of tons of pesticidal plant products each year. In 1972, the United States imported more than 45,350 kg (100,000 lb) of pyrethrum daisy (*Chrysanthemum cinerariaefolium*) flowers (Fig. 10) worth nearly $50,000, obtaining pyrethrum extracts worth more than $8.6 million, and over 0.66 million kg (1.45 million lb) or more than $250,000 worth of whole or powdered roots from *Derris* and *Lonchocarpus* species—the sources of rotenone.

In addition to their direct contributions to industrial productivity, animal species sometimes contribute indirectly to industrial production processes. The use of animals for draft power, particularly in the developing nations, and as sources of fertilizers and fuels were mentioned previously. In industrialized nations, animals frequently serve as laboratory and field subjects for scientific research, the benefits of which contribute to industrial productivity. They are also used for product evaluation and other experimental procedures, much in the same manner as they are used for drug safety testing and evaluation. Perhaps one of the most novel and interesting uses of animal species is as biological control agents to remove noxious, exotic weeds that clog industrial waterways. The costs of mechanical removal of waterweeds from inland water areas are often prohibitive. For example, water hyacinth (*Eichhornia crassipes*) alone covered nearly 1,214,100 million ha (3 million acres) of inland water surfaces in the state of Florida in 1975; the least costly mechanical method of removal of this noxious, introduced weed amounted to an estimated $83.40/ha ($33.75/acre) annually for one lake of 162 ha (400-acres). The organisms suggested as potential biological control agents for such waterweeds include grass carp and other herbivorous fishes, crayfish, ducks, geese, and other birds, and even endangered manatees (Figs. 11-13). Specialized herbivorous insects (those restricted to feeding only on the particular weed being combatted) can also be located from the

Fig. 11. A West Indian manatee *(Trichechus manatus)* feeding on aquatic grass in Florida. Manatees eat large quantities of aquatic weeds and have been used in Surinam and in the Republic of Guyana to keep canals clear of aquatic vegetation. (Photo: N.D. Vietmeyer)

Fig. 12

Figs. 12 and 13. In 1965, 5 full-grown manatees were added to an eastern Florida drainage canal that was clogged with submerged weeds and emergent cattails and reeds (left). After only three weeks, the manatees had eliminated the submerged weeds and cleared the emergent vegetation to the shoreline (above). (Photos: P.L. Sguros)

native habitats of the exotic weeds. An example is the South American flea beetle (*Agasicles hygrophila*) (Fig. 14) imported to the United States from the American tropics to control its native host plant, alligatorweed (*Alternanthera philoxeroides*) (Fig. 15). Prior to the introduction of this beetle, alligatorweed clogged many southern waterways in the United States and prohibited free navigation (Fig. 16).

Fig. 14. The South American flea beetle *(Agasicles hygrophila)* feeding on introduced alligatorweed in the United States. (Photo: Agricultural Research Service, USDA)

Fig. 15. Two United States Department of Agriculture scientists release South American flea beetles in an alligatorweed infested stream in South Carolina. (Photo: B. Bjork, USDA)

Fig. 16. Two fishermen near Lake Pontchartrain, Louisiana attempting to free their outboard motor from alligatorweed. (Photo: Agricultural Research Service, USDA)

In addition to their role in controlling or removing certain pests which inhibit industrial activities, wild species can also be employed to help control pollution by aiding in the removal of pollutants and pesticides from inland waters, soils, or the air. Although microorganisms play an extremely important role in degrading harmful chemicals present in soil or water, many plant species also serve humanity by absorbing inorganic elements. Of course, the primary role that plants play in this process is that of absorbing the tremendous quantities of carbon dioxide (CO_2) produced by combustion of fossil fuels and wood. CO_2 is used during the photosynthetic process, with the carbon being incorporated into sugars and ultimately into other organic compounds (which can then be harvested and utilized by man) and the oxygen (O_2) being released as a by-product, thus replenishing the oxygen consumed during fuel combustion processes. Specific plants, however, such as American cattail (*Typha latifolia*) and water willow (*Justicia americana*), and ironically, introduced pests such as the waterweeds mentioned previously—alligatorweed and water hyacinth—are capable of removing large quantities of nutrients from polluted aquatic environments. For example on a per hectare basis, cattails are capable of removing up to 2,630 kg (5,800 lb) of nitrogen, 1,710 kg (3,770 lb) of calcium, 4,570 kg (10,075 lb) of potassium, and 400 kg (885 lb) of phosphorus from sewage collecting ponds annually. All of these plants possess good nutritional value, and if occasionally removed for nutrient abatement purposes and dried, they might be useful as a source of fertilizers or feedstuffs for domestic livestock. Moreover, sale of such derived products would partially offset the costs of removal operations.

Another way in which species aid us in dealing with the problem of pollution caused by various industrial activities is their role as pollution or "biological" indicators. The endangered Torrey pine (*Pinus torreyana*) of southern California (Chapter 4)

could be employed as a pollution indicator species. The lichen *Hypogymnia physodes* has been used successfully in transplant experiments in Norway designed to assess the fall-out of air-borne pollutants, especially mercury, from a major industrial complex. Snakes have good potential for use as pollution indicator species; like birds-of-prey and other top carnivores they are especially vulnerable to the adverse effects caused by bioaccumulation of pesticides and other harmful chemicals within food chains in natural environments. However, unlike birds, they are usually sedentary and seldom roam farther than a few kilometers during their entire lifetime. Thus, they may be among the most reliable of vertebrate indicator organisms, because there is less risk that they will migrate from contaminated to uncontaminated areas, or vice versa. In the marine environment, various species of bivalve molluscs and macroalgae have proved to be efficient and reliable as biological indicators for study of trace metal pollutants in water and sea sediments. Probably the best known of these indicator species is the edible mussel *Mytilis edulis*, an organism widely distributed throughout temperate waters and which has a well studied physiological system; a wealth of knowledge has accumulated regarding the content of trace metals in its tissues in various waters and its mechanism of metal uptake. It is of interest that most of the 16 species of freshwater mussels (naiads) currently considered endangered in the state of Ohio are potentially useful freshwater pollution indicator species.

In addition to their use as pollution indicators, there are other ways in which wild species may be used as biological indicators. Certain plant species, in particular, could be useful for biogeochemical prospecting. For example, in gold prospecting one of the greatest problems is that very large amounts of soil must be collected in order to obtain a representative sample of the precious metal which may be present in a given locality. In the case of suitable indicator plants, however, much smaller samples need be taken by the prospector since the root systems are capable of "sampling" a large volume of the soil present. In Wales, the grass *Festuca rubra* contained as high as 95 ppb (parts per billion) of gold in their leaves (dry weight), while 40 percent of the other species evaluated also contained gold concentrations which were significantly elevated over the background concentration (3.42 ppb, as computed by doubling the average of the values obtained for the same species studied when collected from a lead-silver mine).

Whether basic necessity or luxury item, good or service, both wild and genetically improved flora and fauna have been and still are exploited to meet the constantly changing needs and desires of the world's people. Yet, we have only begun to understand how to locate and properly use gene resource species to derive new or substantially improved industrial products from them. Meanwhile, the continued harvesting of wildlife products and live animals or plants from populations of rare or endangered species is threatening the continued existence of the unique gene pool resources they offer as well as the industries or businesses based upon them. Moreover, reducing such threatened taxa to the verge of extinction destroys potentially renewable resources which could, in many instances, have otherwise been used to contribute to the productivity of other sectors of the economy. The potential contributions of gene resources in the near and far future, both as sources of new industrial goods or services, and as sources of germplasm for the genetic improvement of particularly useful species, will depend primarily on our present efforts to reduce genetic erosion and to adequately conserve representative samples of genetic materials through conservation of species and their essential habitats.

9

Economics and Extinction

It is impossible to complete this discussion of the contributions of genetic resources to human life and well-being without mentioning the role of economics. Gene resources and *in situ* conserved habitats can and do contribute significantly to economic productivity; but their true contributions are frequently not acknowledged by the economic sector. A focus upon immediate economic returns can result in the extinction or severe depletion of resource populations through failure to conserve and properly manage these biotic resources or their habitats. Moreover, the increased scarcity of gene resources caused by extinction raises important questions about the intergenerational equity of the present generation's method of allocating our biotic resources over time.

Genetic Resources: Price-less But Not Valueless

A major purpose of this study has been to provide information about the unknown or unacknowledged values of various gene resources and the goods or services they provide to society. One may ask, however, why are these biotically derived resources undervalued in an economic sense? Primarily because they are not priced by a market system. A resource, e.g., pure air or water or a gene resource, may have some value to an economy or society; however it will not be considered economically important unless it has acquired a monetary price within the marketplace. A gene resource cannot be priced until it is considered scarce and some level of competitive bidding has evolved to determine its use, and until some method or technique has been developed whereby it (or its products) can be properly fitted into the production process. For this reason, a genetic resource is considered a ''free good'' until it has become scarce in an economic sense. This means that even though it may not be valueless, it is price-less.

Unfortunately, a genetic resource or any other natural resource which has socioeconomic value, but which does not have a price attached to it, cannot be prop-

erly considered within the private economic sector. The problem for conservation lies in our inability to fix a price until a resource has become scarce (or is perceived as such). The true economic value of a genetic resource is often not acknowledged until the species or population which provides it has become biologically rare, severely depleted, or even extinct! For some wild species, e.g., the Passenger Pigeon and the larger baleen whales (Chapter 3), extermination proceeded so rapidly in concert with improved harvesting methods that the increasing biological scarcity of the harvested populations was not transformed into commodity price increases. A second reason that prices may remain low (for an increasingly scarce number of resource populations or species or their products) is that suitable economic substitutes from more common species may proliferate on the market. In the case of the Passenger Pigeon, a variety of other wild and domestic meat-producing species were available for economic use; and in the case of the baleen whales, other suitable species could be harvested instead to supply the edible whale oil. As a result of the lack of overall scarcity of the market commodity (meat or oil), the price of the product specifically derived from the depleted species did not tend to increase even as the species (or its distinct populations) neared extinction! In still other situations, e.g., genes derived from crop and livestock genetic resources, the lack of an appropriate method of evaluating the actual contribution of the derived genetic meterials to an economic production process has thwarted progress in assigning them any monetary values.

Ideally, economic productivity and the welfare of both present and future generations would be best promoted by maintaining a broad diversity of genetic materials and their requisite habitats for future needs, as well as populations of valuable resource species at levels high enough to allow the continuous removal of a sustainable yield of desirable products. At least we should acknowledge that the cost to society (or the private sector) of maintaining a viable breeding population of certain wild species or gene resource populations is not very great in comparison to the economic costs which will be incurred subsequent to, and as a result of, their extinction. If appropriate analyses were conducted for each species, it is very likely that we would decide that we would not wish to extinguish most of them on the basis of purely economic grounds. However, at present, given the state of art of current economic theories and practices, such analyses cannot be easily accomplished. Progress in correcting these problems must be made soon, before a multitude of endangered gene resource populations and wild species disappear completely from the earth, as so many others have vanished before them.

How Much Are Natural Areas Worth?

Another important problem in the conservation of genetic resources is undervaluation of the socioeconomic benefits which accrue from the retention of land or water habitats in an undeveloped or preserved state. An effort is often made to evaluate the relative worth of alternative, incompatible uses of land or water areas when development interests come into conflict with those of conservationists or society as a whole. The most commonly employed evaluative tool is benefit-cost analysis, i.e., determination (and adoption) of the investment alternative that demonstrates the highest net benefits (the net difference between benefits and costs). In theory, this seems to be a good tool for decision analysis; at least, its use would

seem preferable to the alternative of merely allowing land or water development to proceed without any stated economic justification, such as typically occurs in the private sector with the gradual loss of individual parcels of land to urban residential expansion or the piecemeal conversion of a forest into farms and ranches. In practice however, there is no practical way to safeguard the public interest through use of this technique in the absence of appropriate economic or legal guidelines to the contrary. Even if nondevelopment were in the public interest, it is difficult to organize and represent the diffuse interests of the general public; on the other hand, it is relatively very easy for the few people or business interests who are sponsoring a development project to organize and economically promote their investment alternative.

Partly for this reason, consideration of *in situ* conservation of natural environments as an investment alternative is not a common practice in conventional benefit-cost analysis. Some of the guidelines used for benefit-cost analyses conducted by various entities in the past have endeavored to incorporate intangible and presumably incalculable social or environmental costs associated with each development alternative. Unfortunately, for most genetic resource products (or for services provided by natural areas), there are no well-developed markets to which one can turn for needed price information. Moreover, there is usually little agreement on what constitutes a "cost." On the other hand, when social or environmental costs are merely listed as intangibles, there is a tendency for them to be ignored in the decision-making process. In the absence of precise calculations and the determination of dollar equivalents—a difficult task indeed when determining the loss of a species or a gene resource for which no spot market exists—intangible costs cannot be easily weighted against the projected monetary benefits of a proposed development. As a consequence, benefit-cost analysis has proved to be more a means of justifying one development option over another, rather than controlling development in any sense in order to retain an effective balance between use and preservation of natural resources. Thus, one by one, developments are proposed, the development alternatives are evaluated, the social costs of habitat losses or extinction are ignored or casually considered, and the decision to develop is given the go-ahead, actually on the basis of incomplete economic information! It is by this gradual process of land conversion that entire ecosystems and wildlife species have disappeared. In the absence of any effective decision-analysis tool or of guidelines that dictate restrictions on the development process, habitat destruction has become the leading case of species extinctions and genetic losses both within the United States and abroad.

Some enterprising environmental economists and biologists have endeavored to evaluate preservation of natural areas as an alternative option for development decisions. These studies have focused on methods that can be used to evaluate economically or to assign a monetary value to the socioeconomic benefits of natural ecosystems. These benefits include:

- Photosynthetic fixation of solar energy;
- Production of biomass and consequent provision of foods, medicines, or industrial raw materials;
- Absorption and breakdown of pollutants, including the degradation of organic wastes, pesticides, and air and water pollutants;
- Cycling of essential nutrients, e.g., carbon, nitrogen, oxygen;
- Production and binding of soil;

- Maintenance of the oxygen-carbon dioxide balance;
- Regulation of radiation balance (temperature) and climate;
- Role of natural environments as *in situ* reservoirs of genetic diversity, particularly the maintenance of environmental forces and species that influence the acquisition of useful genetic traits in economic species; and
- Recreational-esthetic, sociocultural, scientific and educational, or historical values of natural environments.

All of these social or environmental benefits provided by natural areas are external to the conventional economic framework; thus to the extent that these benefits are adversely affected by development processes, only some of the true costs of development are actually considered in conventional benefit-cost analyses.

Most of the studies that have provided a benefit-cost analysis for a preservation or conservation alternative have focused on the dual approach of incorporating economic or environmental costs ignored during their initial calculation for a proposed development, and calculation of the recreational-esthetic benefits accruing from the preservation option, as far as possible. Some studies, such as the Hells Canyon hydroelectric dam and White Cloud Peaks mining studies, indicated that proposed development projects were often indefensible on purely economic terms, even without inclusion of any or all of the monetary losses which would be sustained due to the destruction of recreational opportunities. In other cases, the values of various land and water habitats for recreational or esthetic purposes have been assessed and included. For example, the annual value (present worth) of 122 km (76 mi) of Kentucky streams for fishing was worth $223,000 (an average of $1,824/km or $2,934/mi) in 1969; and the value of a stretch of relatively undeveloped lake shoreline in Washington state has been demonstrated to outweigh the economic costs associated with foregoing the option of more intensive shoreline development. Similarly, a proposal which would destroy only 5 percent of the Mississippi waterfowl flyway (43,500 ha or 107,490 acres) in 1975 was projected to result in a hunting and recreational loss valued at $56 million annually (present value discounted at 6.38 percent); this is the equivalent of $1,287/ha ($521/acre).

More interesting, however, are the recent attempts to calculate the cost of economic losses incurred due to the loss of some natural habitat, or the cost of duplicating some of the "free" services of wetlands or estuaries to society in the event of their destruction. A study of wetlands in Massachusetts estimated the capitalized value (at 5.375 percent) of one hectare at $147,900 ($59,850/acre) for wetlands with a high capacity for provision of water supply, flood control, wildlife, and recreational and esthetic benefits, while a single hectare with only a low capacity for wildlife and recreational and visual benefits was estimated at $1,728/ha ($700/acre). Comparison of the value of undeveloped wetlands with the prevailing purchase price for development on a per hectare basis resulted in the conclusion that roughly 90 percent of the remaining wetlands in the state of Massachusetts were better left in a preserved state for the benefit of society than developed for the benefit of a few. Many other important benefits were not considered in this analysis. Yet another study has attempted to calculate the gross benefits derived from conservation in a relatively natural state of a Georgia tidal marsh. The value of each unit area of marsh for providing primary productivity which supports offshore commercial and recreational fishing industries was calculated at $4,938/ha ($2,000/acre) (present value discounted at 5 percent in 1972). Alternative consideration of the tertiary waste

treatment benefits provided by default by marshes, without any cost to society, were calculated at roughly \$123,500/ha (\$50,000/acre), and for removal of excess phosphorus alone, \$47,000/ha (\$19,028/acre). Although it is true that industries do not now have to pay for these services, if marshes were not present to provide them, the environmental overload caused by the pollutants would eventually have to be taken care of by society. Otherwise, other serious costs would be incurred, such as increased medical costs due to human health problems, food productivity losses due to destruction of offshore fisheries, etc.

As these studies indicate, many of the natural environments that are currently being destroyed or irreversibly altered might produce far more benefits for the local populace and society as a whole if conserved and used in a more natural state than if converted to a use which would produce more rent (profit) for a private landowner or development interest. It also suggests that our national parks, wildlife refuges, wilderness areas, and other publicly appropriated natural areas may be grossly undervalued in a socioeconomic sense. The true value of these national treasures should be more appropriately evaluated in terms of the benefits they provide to commercial fisheries and wildlife interests, to hunters and other sportsmen, and to the industries and people who live in populated areas nearby who unknowingly use the clean water and air obtained from them and exploit their waste removal capacity. Perhaps the true economic productivity of various ecosystems should be evaluated, and an appropriate conservation tax placed on the revenues obtained from such uses of nature's services. Additionally, one might advocate the imposition of a conservation tax or penalty to accompany the purchase of particularly valuable natural areas for development—as payment for the foregone opportunity of providing the society at large with these benefits. Such conservation tax funds could then be used to facilitate preservation or conservation of some areas in return for the option of developing others to serve more traditional economic interests.

Economic Causes of Extinction

Although some species or populations are biologically more vulnerable to extinction than others, most of the extinctions that have occurred in recent times were induced by human activity. In an ultimate sense, human-induced extinctions typically result from the combined attitudes and desires of a great number of people. Sometimes extinction occurs for a purely psychological reason, e.g., out of "spite," to establish that one can exert control over nature, or for the desire to exclusively "own" an entire rare plant or animal species. However, since human desires and attitudes are most often expressed in the form of consumer demand in the marketplace, it would be instrumental to more carefully examine economic causes of extinction.

As demonstrated by many of the case studies provided previously, unbridled economic development (or an exclusive focus on immediate economic productivity) facilitates the demise of gene pool resources. Such biologically based resources can be extinguished or destroyed both directly through overharvesting and indirectly through destruction or alteration of their requisite habitat. Extinction, whether it results from direct or indirect extermination processes, is actually an economic externality or external cost of established or preferred production alternatives. An external cost is any social or environmental cost not accounted for by ordinary market pricing mechanisms or supply-demand interactions. As such, extinction is only rarely

an intentional event. More often, it is an inadvertent or unplanned result of the pursuit of certain production alternatives, even though the ultimate result—the irretrievable loss of a valuable species or gene resource—is nevertheless the same.

Open-Access Exploitation: Direct Extermination by Overharvesting

In cases of direct extermination through overharvesting of a resource population or species over time, the most vulnerable species or populations are those to which harvesters are allowed open or unlimited access. In situations of free or open access to harvesting grounds, extinction occurs because the private or collective (public) owners fail to recognize the value of retaining a breeding population or gene pool for the perpetuation of the resource. The economic uses of species which can result in direct extermination are categorized in Table 1.

The phenomenon of open-access exploitation is most commonly referred to as "common property resource" exploitation. A common property resource is a publicly owned commodity which belongs to no one in particular, yet which may be harvested by anyone. In the absence of protection or regulation, common property resources are vulnerable to extinction or depletion because no single harvester has the right to prevent the others from sharing in the exploitation of the resource, nor does any single user have an incentive, due to lack of ownership rights, to take personal responsibility for conservation of the resource base. Thus, when consumer demand rises, more harvesters will be encouraged to enter the process, and each harvester will tend to take more for his share. As demand continues to outstrip available supplies, and fewer and fewer reproductive individuals are left in the resource population, it will inevitably near extinction. Usually as the population reaches this point, commercial extinction of the extractive industry occurs before biological extinction of the resource species; but in many instances extinction has occurred long before the demise of the industry. Reasons include those mentioned previously for the baleen whales, i.e., technological improvements in harvesting methods, and the economic substitutability of more common species. The process of biological depletion and, especially, extinction due to overexploitation, is typically referred to as the "tragedy of the commons."

Despite the amount of attention paid to the common property resource issue, many species or populations threatened by direct overharvesting reside instead on privately owned property. Even if, as in the United States, animal wildlife is in principle considered as a publicly owned resource, if a population resides on private lands (or in private waters), it is relatively difficult for harvesters to obtain access to the harvesting grounds. For this reason, it has been suggested that privately appropriated resources are not vulnerable to extinction or depletion as are commonly owned resources; since the person who owns the land can usually control access to the resource, in theory the supply of the desired product can be regulated. In practice, however, privately owned resources are also vulnerable to depletion or extinction because people who control access to the land (water) may not be aware of the value of the resource in question or may not have an interest in conserving it, particularly if they wish to use their lands (waters) for some other production alternative. Moreover, if a species or gene resource population is highly valued on the

TABLE 1. Human-Induced Causes of Direct Extermination

Species Harvested or Hunted For:	Examples of Threatened or Extinct Taxa*
1. Food (meat, eggs, fats & oils, etc.)	Kaluga*—caviar & fish Green sea turtle—meat, eggs & oil Great Auk—meat & eggs (extinct) Blue whale—edible oil & meat
2. Industrial products (oils, fats, etc.)	Sperm whale—sperm oil
3. Forest products & firewood	Guatemalan fir—forest products & firewood Chilean false larch—forest products (lumber)
4. Fashion industry (feathers, furs, skins & hides, fleece, jewelry, cosmetics, etc.)	Chinchilla—furs Snow leopard—furs Chinese Egret—feathers Crocodiles—skins/hides Hawksbill turtle—shell jewelry & oils for cosmetics Vicuña—fleece & skins
5. Souvenir and curios trade	Mountain gorilla—hands (ash trays); head (curios)
6. Live plant & animal trade (for plant dealers & florists; for animal dealers, pet trade, zoos & research institutions)	Arizona golden barrel cactus—live plant trade Scarlet-chested Parakeet—pet trade Indigo Macaw—pet trade Chimpanzee—zoos, biomedical research Cotton-top tamarin—biomedical research & pet trade Woolly monkey—pet trade & research
7. Medicinal & folk medicinal trade	Indian rhinoceros—rhino horn (folk) Mhorr gazelle—bezoars (folk) American ginseng—herb (folk)
8. Personal & museum collecting	Paradise birdwing butterfly Queen Alexandra's birdwing butterfly African elephant—ivory for collector's items
9. Sport & recreational hunting (trophies, skins)	Saudi Arabian dorcas gazelle Asiatic lion
10. Removal of alleged pests**	Eastern cougar—predatory pest Grizzly bear—predatory pest Carolina Parakeet—competitive pest (extinct)

Sources: Prance and Elias, 1977; IUCN *Red Data Book,* vols. 1-4.
*For some of the examples, there is more than one causal factor.
**Although these species are being directly exterminated, the major reason they are considered as pests is related to indirect extermination categories, such as habitat alterations for agriculture, grazing and ranching, or urban purposes.

open market, many people who control access to specific harvesting grounds will willingly accept a compensatory fee from harvesters in return for access to the harvesting grounds or for removal of individuals from the resource population(s).

An excellent example of this is the current status of many endangered ornamental cacti in the southwestern United States. Some cactus populations have become extinct or have been decimated because ranchers and other private landowners have

allowed harvesters access to their land. Some landowners view all cactus species as pests which interfere with cattle-raising or other ranching concerns, while others are unaware of the value of rare and endangered cacti to collectors, or of ornamental cacti to the landscaping business. Thus they have little or no interest in conserving or retaining an adequate-sized breeding (reproductive) population of such endangered species. Even if they are aware of and care about the important role that they can play in conserving these resources, there is always the threat of illegal poaching. As consumer demand increases for a particular resource or its product, the increase in prices will encourage more and more poachers to risk illegal harvesting ventures. Thus in many situations, privately controlled resources are just as vulnerable to depletion or extinction as common property resources. The well-known environmental economist, S. V. Ciriacy-Wantrup, has observed:

> Common property of natural resources in itself is no more a tragedy in terms of environmental depletion than private property. It all depends on what social institutions—that is, decision systems. . . ,—are guiding resource use in either case. Effective social institutions to conserve common property resources have been developed for the administration of public forests in many countries. The same is true for the conservation of game and fish whether by primitive tribes in pre-Colombian America or modern game-management departments. Agricultural land held in common by villages in medieval Europe was conserved by institutions based on custom and law before private property and the profit motive broke up these decision systems. During the colonial periods of the 18th and 19th centuries the spread of private property rights in resources did not prevent serious depletion of forests, range and agricultural land in many parts of the world (1971, p. 43).

An excellent present-day example of the successful conservation of a common property resource is that of the communal ownership of most of the forests of the Totonicapân and San Marcos areas above 2700m in the Guatemalan highlands. Whereas many of the highland forests there have been or are being destroyed, the Totonicapân-San Marcos forests have diminished very little during the three decades from 1932 to 1972. Different parcels of these forests are owned by different Indian villages, townships, or kinship groups, and each is managed and protected for the production of the highly-esteemed wood of *Pinus ayacahuite*—the principal source of cheap furniture wood for the whole country. Because the Indians use the money obtained from sale of pine products to purchase their imported food items, they vigilantly protect their forests from encroaching cultivators and would-be "tree poachers." In contrast, an excellent example of the destruction of centuries-old systems of limited access to communal fishing grounds is that of the demise of marine conservation methods on many Pacific islands in Oceania. The traditional fishing practices of Polynesians and other native peoples once effected adequate conservation of renewable marine resources through limited entry. However, these methods for conserving the productivity of communal fishing grounds have been and are being destroyed throughout Oceania as a direct consequence of Western influence; as private property concepts have become instituted, the marine ecosystems have become increasingly overexploited.

Thus, whether a number of private landowners are attempting to maximize their individual revenues or a nation or group of collective resource owners are attempting to maximize productivity for all the people or consumers, the impact on the resource population is often the same. Furthermore, whether the biotic resource is maintained on a privately appropriated habitat in a decentralized (private enterprise) economy

or on the "commons" or public lands in a centrally planned or other economy, it will be vulnerable to extinction whenever consumer or popular demand is high enough to encourage the harvesting of more individuals than the population or species can produce to sustain itself. The major difference between the two alternatives is that if a private owner is conservation-minded, he or she can more quickly and easily exert control over the process by limiting access to the harvesting grounds than can a group of legislators or other decision-makers acting on behalf of the public interest or society as a whole. In either case, if access is limited and the resource species or population is offered protection, there will be a tendency for poaching to occur as the price of the resource or its product increases. Considering the very high prices paid for certain unique or rare species or species' products, it is no wonder that so many are endangered today (Table 2 provides some examples from the live animal trade). Under conditions of high consumer demand, regulation or control over the source of the supply (i.e., the harvesters) is often impossible or ineffective. Moreover, whenever consumer demand is very strong, the costs associated with protecting or maintaining illegally traded endangered species or specific gene pool resources often climb precipitously. In such instances then, our last resort may be to attempt to educate consumers about their role in the supply-demand process, urging them to reduce or halt their consumption of these species or their products. Since this is rarely attempted, a great many species or populations directly harvested for economic purposes are currently extinct or endangered.

TABLE 2. Sample Prices Paid For Some Live Birds and Reptiles in the United States During the 1970's†

Common & Latin Names	State (Size of Animal)	Retail Price(s)	Date
Birds:			
Great Sulfur Crested Cockatoo *Cacatua galerita*	IND	$1500	1977
Hyacinth Macaw *Anodorhynchus hyacinthus*	Various	$1,500-12,500	1979
	NY/CA	$4,850-10,000	1977
	FL	$550	1971
Blue and Yellow Macaw *Ara ararauna*	Various	$950-2,000	1979
	NY	$500-2,000	1977
	FL	$125	1971
Scarlet Macaw *Ara macao*	Various	$950-2,500	1979
	DC/NY	$750-1,250	1977
	FL	$125	1971
Military Macaw *Ara militaris*	Various	$500-1,600	1979
	NY	$650	1977
	FL	$150	1971
Reptiles:			
*Gopher tortoise *Gopherus polyphemus*	FL (—)	$10	1979
	IND (6-10″)	$35	1977

TABLE 2. (Continued)

Common & Latin Names	State (Size of Animal)	Retail Price(s)	Date
*African pancake tortoise *Malachochersus tornieri*	IND (4-6″)	$45	1977
*American alligator *Alligator mississippiensis*	IND (3-6′)	$200-300	1977
*Beaded lizard *Heloderma horridum*	IND (2-3′)	$200-300	1977
Gila monster *Heloderma suspectum*	IND (9-17″)	$225	1977
*Rhinoceros iguana *Cyclura cornuta*	IND (1-4′)	$150-200	1977
Emerald tree boa	NY (—)	$650	1979
Corallus canina	CA (3-5′)	$400	1978
	CA (3-6′)	$85-125	1971
Anaconda	CA (7′)	$200	1978
Eunectes murinus	CA (8′)	$150	1971
Green tree phython	CA (3-4′)	$350	1978
Chondropython viridis	IND (3-5′)	$400	1977
African rock python	NY (15′ female)	$1,250	1979
Python sebae	IND (6-15′)	$250-850	1977
Timor python	CA (3′)	$500	1978
Python timoriensis	IND (4′)	$400	1977
	CA (—)	$1,000	1971
Mexican milksnake	NY (1-2½′)	$150-250	1979
Lampropeltis t. annulata	CA (2½′)	$200	1978

*An endangered or protected species.
†Prices for macaws are provided in Nilsson and Mack (1980)—cited in Ch. IV. Other sources: NY-1979 = Rochester Reptile (Hilton, NY) price list; CA-1978 = Zoological Imports & Products, Inc. (Inglewood, CA) price list; IND-1977 = Midwest Reptile and Animal Sales, Inc. (Fort Wayne, IN) price list; CA-1971 = Hermosa Reptile and Wild Animal Farm, Inc. (Hermosa *Beach, CA) price list. Florida gopher tortoise price supplied by Lt. Col. Brantley Goodson (Florida Game and Fresh Water Fish Commission).

External Costs: Indirect Extermination

In cases of indirect extermination, extinction or depletion of a resource population occurs as an external cost of established or preferred production alternatives, or of efforts to enhance economic productivity. Table 3 lists the categories of human activities that indirectly result in the extinction or depletion of species or gene pool resources; most of these causal factors are directly related to the pursuit of economic activities.

As an external cost, extinction is usually an unintended side-effect of land or water development or business pursuits. As such, the loss is not recognized in an economic sense—either as a monetary cost which should be borne by the causative agent or business, or even as a cost at all. However, when a species or population becomes endangered or extinct as a result of such indirect mechanisms, it is a very real social cost—a cost which, by default, must be borne by all members of society. This is particularly true when the endangered or extinct species involved has known or potential value for some alternative economic or social use, e.g., the biomedical research value of the many disappearing nonhuman primates; the food-producing value of the shortnose sturgeon, the longjaw cisco, and the walia ibex; and the potential breeding value of the Hawaiian and Laysan ducks, the Indian wild ass, the Asiatic buffalo, and Texas wild-rice. These biological losses translate into economic losses for other business concerns as well as for future generations of human beings. The mere depletion of a beneficial species as an external cost of one enterprise can produce disastrous results for another entrepreneur. One well documented case of such an external cost is the demise of native bee populations in New Brunswick, Canada as a result of spraying organophosphorus insecticides to control the spruce budworm (*Choristoneura fumiferana*) in timber-producing regions. Local blueberry farmers, who depend on native bees to pollinate their crops, sustained the economic losses of crop failure rather than the forestry concerns which were indirectly responsible for their losses. This is the nature of an economic cost which is external to the conventional economic framework.

Consideration of such external costs of economic activities need not be limited to threatened or extinct species or populations. Nearly all of the widespread losses of crop and livestock gene resources can also be attributed to indirect extermination processes. The major cause of such losses is their displacement by high-yielding, genetically improved crop varieties and livestock breeds, an activity commonly associated with habitat alterations in traditional agro-ecosystems. The most pertinent example is that of the widespread adoption of modern cultivars developed as a part of the Green Revolution strategy for enhancing crop productivity in the developing nations; although introduction of these modern HYV cultivars has allowed the transformation of traditional farming systems into more modern, monocultural agro-ecosystems capable of producing greater, immediate economic returns, they have also been responsible for the destruction of the very crop genetic resource base which, in part, allowed their development in the first place. In other instances of crop (or livestock) genetic erosion, gene resources have been extinguished because of habitat alteration or destruction which occurred during the transformation or use of the land for alternative economic purposes, e.g., tourism, urban-industrial expan-

TABLE 3. Human-Induced Causes of Indirect Extermination

Species Eliminated Due To:	Examples of Threatened Species*
1. Habitat alterations—urban-industrial	Abbott's Booby—phosphate mining Florida Everglade Kite—urban expansion Houston toad—urban-industrial expansion San Diego mesa mint—urban expansion
2. Habitat alterations—agriculture & grazing	Colombia white-tailed deer—conversion to agriculture Asiatic buffalo—agriculture & grazing Walia Ibex—agriculture & grazing Attwater's Prairie Chicken—agriculture
3. Habitat alterations—silviculture & logging	Orangutan—logging of tropics Drill—logging of tropics Ivory-billed Woodpecker—logging in southeastern U.S. Venus' flytrap—silvicultural practices
4. Introduced/exotic predators (feral dogs, cats, pigs; mongooses, rats, etc.)	Hawaiian Duck—cats, rats, mongooses Galapagos tortoises—dogs, cats, pigs, rats
5. Introduced/exotic competitors (feral goats & sheep; rabbits, exotic wild animals or plants, etc.)	Laysan Duck—European rabbits Galapagos tortoises—goats, donkeys Hawaiian animals and flora —exotic plants
6. Introduced/exotic parasites & diseases	Longjaw cicso—parasitic sea lamprey Crested Honeycreeper—avian diseases Indian wild ass—animal diseases
7. Pollution, pesticides & industrial accidents	Peregrine Falcon—DDT pesticides Shortnose sturgeon—lake pollution Imperial Pheasant—herbicide spraying during Vietnam war
8. Warfare & military operations	Indochinese gibbon—Southeast Asia Douc langur—Southeast Asia Giant sable antelope—Angola Kouprey—Southeast Asia
9. Removal of coevolved or other species needed for survival	Black-footed ferret—removal of prey (prairie dogs/ranching) Cuban Hook-billed Kite—removal of prey (snails for market) Tambalacoque tree—extinction of Dodo (presumed seed disperser)
10. Removal of barriers preventing hybridization with close relatives	Red wolf—hybridization with coyotes and feral dogs Greenback cutthroat trout—hybridization with introduced rainbow trout Italian Gray Partridge—hybridization with introduced partridge subspecies

Sources: Prance and Elias, 1977; IUCN *Red Data Book,* vols. 1-4; Temple, 1977.
*For most examples, there is more than one causal factor.

sion, logging. Consider the following examples* of crop genetic erosion due to habitat destruction or alteration:

- In 1959, W. C. Gregory was sent to South America to collect peanut germplasm resources for the United States. In 1968, W. R. Langford and R. Hammons were sent back to Brazil and Argentina to locate germplasm from some of the same areas which had previously yielded useful gene resources. When they returned, they reported that an important collecting area they were instructed to locate for resampling had been destroyed by bulldozers working on a road construction project.
- When a garden pea virus became a problem in the northwestern United States, a plant collector was dispatched to the Mediterranean, a center of diversity for peas, to collect wild gene resources. Even though they were previously abundant there, the collector found them difficult to locate because most of their natural habitat overlapped with historic sites where wild plants had been systematically uprooted to make the attractions more esthetically pleasing to tourists.
- Prior to the flooding of the Aswan Dam in Egypt, officials asked natives who were being relocated to take their best safflower varieties with them. Unfortunately, they decided upon the genetically improved, but highly uniform varieties introduced from the United States a few years earlier. When the dam flooding occurred, the ancient landrace varieties, representing thousands of years of human breeding efforts, were destroyed.
- The 'Travois' variety of alfalfa (*Medicago falcata*) owes its cold resistance and superior root proliferation qualities to the wild yellow-flowered alfalfas of Russia which were collected in 1908 and 1910. When John Creech returned recently to cover the old collecting grounds, he found them covered with houses and other types of urban development.
- Wild cocoa (*Theobroma*) germplasm from Ecuador has provided valuable resistance genes for certain cocoa diseases. However, most of these wild populations no longer exist, since their habitat has been transformed into forms of brushy pastures or has been destroyed by oil drilling activities initiated by U.S. firms.

Crop gene resources are also directly exterminated; as an example, wild pear trees (*Pyrus serotina*) were abundant and easily collected in Japan in 1961, but most of these wild stands no longer exist because of their value as a source of charcoal. However, most of the documented examples of genetic erosion in crops involve indirect extermination processes.

Of all the direct and indirect causes of extermination induced by mankind, today the leading cause is habitat alteration for purposes of converting land to more immediately recognized, productive uses (Fig. 1). If demand for an alternative economic use of habitat is very low, it will probably remain unaltered; thus, the environmental conditions necessary for the maintenance and survival of the gene resources or wildlife populations which depend on that habitat will, at least potentially, be ensured. However, if a previously "useless" habitat becomes valued as a

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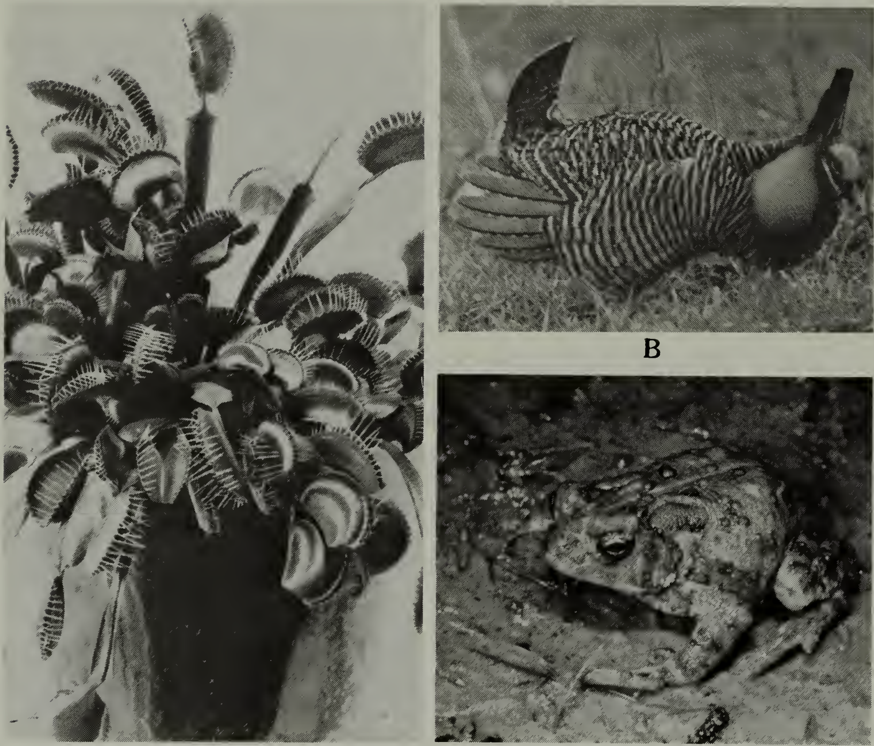
*All of these examples, with the exception of the *Theobroma* (cocoa) example provided by E. P. Imle of the USDA International Programs Division, were supplied by John L. Creech of the U.S. National Arboretum.



B

A C

Fig. 1. Habitat encroachment has been the principal cause of the decline of these U.S. species: A. Venus' flytrap *(Dionaea muscipula),* threatened by silvicultural and logging operations in the southeastern United States. (Photo: USDA), B. Attwater's Prairie Chicken *(Tympanuchus cupido attwateri),* endangered due to cultivation and overgrazing of its prairie habitat. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI), C. Houston toad *(Bufo houstonensis),* endangered by loss of habitat from urban-industrial expansion. (Photo: R. Thomas, U.S. Fish and Wildlife Service, USDI).

site for some alternative economic venture, the resident populations are likely to become depleted or exterminated as a result of ensuing habitat changes. In most modern, industrialized economies, land use patterns are typically dictated by the rent-producing capacity of the parcel of land in question, regardless of its value to society in a preserved state. Thus, in the absence of zoning or other land use planning mechanisms, decisions to develop or preserve land tend to be guided solely by economic criteria—criteria which dictate the most profitable uses of land when held in private ownership. From an economic point of view, the ''highest and best use'' of land is associated with urban-industrial, and secondarily, residential, property. Thus, if prime agricultural land or a valuable wildlife habitat is being encroached upon by industrial, urban, or residential developments, in most cases the farmers and wildlife enthusiasts will lose out, and the land they value for their own purposes will be gradually replaced by concrete and buildings. Similarly, if forests or deserts can be put to more monetarily productive uses for private landowners, such as

agriculture, grazing, mining, or forestry, the land will eventually be turned over to its "higher" and "better" use.

If the land cannot be employed for these more immediately productive purposes, it is often euphemistically referred to as "barren and waste." To the ecologist, wildlife biologist, or conservationist, no habitat or ecosystem would be considered as such; moreover, these people would probably opt to reverse the ranking of these lands use alternatives! Even though it is evident that the direction of the rank order would be determined on the basis of one's particular attitude and priorities, from a practical perspective the economic view of land use usually prevails in conflicts over development vs. preservation decisions. In the view of the conservationist who seeks a harmonious balance between development and preservation of natural resources, it now seems difficult to conclude otherwise than that there are already too many cities, industrial parks, dams, mines, ranches, farms, timber operations, and other developments, and too few natural areas left to sustain gene resources and dwindling wildlife populations. The automatic and seldom questioned process of shifting land from lower to higher rent- or profit- producing uses for the benefit of certain users or industries demonstrates our general disregard for the broader socioeconomic value of these biotic resources—renewable resources which if allowed to survive could be used for a variety of other economic purposes.

Another prevalent cause of extinction or depletion is the introduction of exotic predators, competitors, and parasites or diseases. Species endemic to islands, or those which have a very restricted distribution on mainland areas, are especially vulnerable to the adverse ecological consequences of exotic introductions. Since native species have not interacted with such alien organisms during their evolutionary past, they usually lack the appropriate adaptive behaviors, defensive chemicals, or other mechanisms they need to contend with introduced species. On the other hand, when exotic species are transplanted to new environments, they often manage to escape most of their native predators, competitors, parasites, and diseases. Once released from the biotic factors which had previously controlled or checked their population growth, some exotic species attain a pest status in a new, suitable environment.

Given such a competitive edge over native flora and fauna, exotics can (and do) contribute to the extinction or decline of native species, Thus, even though most subspecies of the giant Galapagos tortoises somehow survived the depredations of whalers, sealers, fishermen, and buccaneers in centuries past, they may not survive the adverse ecological impact of the exotic animals these adventurers brought with them. Most subspecies of these gigantic reptiles are currently threatened by such competing herbivores as feral goats, donkeys, and cattle, while their eggs and young are consumed by black rats and feral cats, dogs and pigs. Likewise, a number of African ungulates have declined due to introduced cattle diseases, while their domesticated competitors suffer from the native animal diseases to which the wildlife are immune. Moreover, many Hawaiian bird species are extinct or currently threatened by avian diseases brought to the islands along with exotic game and cage-birds; other Hawaiian animal species have barely survived the impact of such introduced predators as cats, rats, and mongooses. The native Hawiian flora is being outcompeted by introduced ornamentals and weeds, and decimated by exotics such as feral pigs and feral goats. In most cases exotics are introduced to new environments primarily for economically related purposes. Horticulturalists and landscapers in-

troduce exotic plants; foresters, exotic timber trees; hunters, their favorite exotic prey; farmers and ranchers, alien crops and livestock; and pet dealers, exotic pets. When all has been said and done, the biological control expert is often called upon to locate exotic parasites and predators to control the well established exotics! (Which may often, in turn, require biological control agents.)

Considered altogether, the remaining indirect causes of extinction have threatened or caused the extermination of far fewer species than has either habitat alteration or introduced exotics. Pollution, pesticides, and industrial accidents such as oil spills have yet to claim a single taxonomically known species, and no currently endangered species is threatened solely as a result of one of these factors. However, many birds-of-prey, including the Peregrine Falcon, the Bald Eagle, and the Brown Pelican (Fig. 2), have suffered from the adverse effects of DDT and other pesticides. Fat soluble pesticides such as DDT become increasingly concentrated in living tissues

Fig. 2. The widespread use of DDT and other chlorinated hydrocarbons indirectly contributed to the decline or near extinction of these native American birds: A. Bald Eagle *(Haliaeetus leucocephalus).* (Photo: W.S. Keller, National Park Service, USDI), B. Peregrine Falcon *(Falco peregrinus).* (Photo: M. Smith, U.S. Fish and Wildlife Service, USDI), C. Brown Pelican *(Pelecanus occidentalis).* (Photo: A. Wetmore, U.S. Fish and Wildlife Service, USDI).

as they are transferred through the food chain; and top carnivores, such as predatory fish, birds, and mammals, are therefore among the most vulnerable to their effects. Studies have demonstrated an inverse correlation between eggshell thickness and concentrations of fat-soluble pesticides in the eggs of predatory birds. Since thin-shelled eggs cannot usually be successfully incubated, fat-soluble pesticides have been held responsible for the decline in reproductive success of many birds-of-prey.

Warfare, even though not an economic activity *per se*, frequently involves disputes over land and water resources, and in the process of waging war some of the disputed territory is destroyed or severely altered. Additionally, animals are frequently sought as sources of food, or they are used for target practice by military personnel. During the recent war in Indochina, many rare and common species not only suffered from habitat losses, but also from the direct toxicity of and habitat alterations induced by the spraying of herbicides. As a consequence of warfare in Southeast Asia and many parts of Africa, a number of formerly rare or threatened species may now be extinct or near extinction. Many of these, like the douc langur (*Pygathrix nemaeus*), a nonhuman primate that inhabits Laos and Vietnam, and the kouprey, (*Bos sauveli*), a cattle relative, have potential value for certain economic purposes.

Finally, some economic activities and environmental manipulations can result in losses of species or populations through the removal of other species necessary for their survival, or by the removal of ecological or geographical barriers which precluded hybridization between closely related taxa. In the latter case, barriers may be obviated by the mere transport of individuals of one taxon to a related taxon's native environment (Italian Gray Partridge, *Perdix perdix italica*; many native U.S. trout species). Or changes may be wrought in the environment such that previously separated species are brought into close proximity with one another (the red wolf, *Canis rufus* (Fig. 3), now hybridizing with coyotes and feral dogs). In the former instance, the most vulnerable taxa are those which have coevolved with another species to the point where removal of one species threatens the existence of the other; for example, it has been suggested that the tambalacoque tree (*Calvaria major*) on the island of Mauritius has become endangered because of the extinction of the Dodo (*Raphus cucullatus*), a very large, flightless bird which presumably served as the primary seed-dispersing agent of that species. On the other hand, species which have evolved special morphological features, behaviors, or other adaptations that allow them to exploit a single prey or host species are particularly vulnerable to a reduction of the population size of the required species. Thus, the black-footed ferret (*Mustela nigripes*) (Fig. 4) has declined as a result of massive poisoning programs launched to eliminate its natural prey (prairie dogs) which are considered pests by many U.S. cattlemen. Similarly, the Cuban Hook-billed Kite (*Chondrohierax uncinatus wilsonii*), which depends primarily on *Polymita* tree snails for food, is now very rare due to the huge quantities of beautiful shells taken by collectors.

Are Living Resources Becoming Scarce?

During the last few centuries of technological advancement, widespread industrialization, and rapid human population expansion, worldwide extinction rates have increased dramatically. Considering only the major species and subspecies of mammals and birds—the largest vertebrates and therefore those most intensively

Fig. 3. Today fewer than 100 pure bred red wolves survive in a small coastal area in Texas and Louisiana, and this population is being genetically swamped as a result of hybridization with other wild or feral canids. (Photo: C. Curley, U.S. Fish and Wildlife Service, USDI).

Fig. 4. The black-footed ferret *(Mustela nigripes)* is endangered as a result of loss of habitat and elimination of its principal prey—prairie dogs. (Photo: L.C. Goldman, U.S. Fish and Wildlife Service, USDI).

followed over time—extinction rates have jumped at least tenfold during the last three centuries. Among the birds alone, the loss rate averaged only one every ten years from 1651 to 1750; but during the next century the extinction rate climbed to one taxon every 3.5 years; and by the century ending in 1950, more than one species or subspecies was being exterminated annually. Today it is feared that the rate is even two, three, or five species or subspecies per year. This is only the tip of the iceberg, some species of reptiles, amphibians, fish, insects, plants, and microorganisms—most unknown to the scientific world—are now believed to be disappearing annually. It has been conservatively estimated that from one-half to two-thirds of the remaining moist tropical forests of the earth will have been destroyed by the end of this century. Along with these biotically diverse habitats, an estimated 500,000-600,000 of both known and unknown species—some guess more than a million—will also vanish. This means that out of roughly 5-10 million species now thought to inhabit the earth, possibly as many as we have been capable of scientifically naming to date will be extinct by the year 2000—about half of the biotic diversity of which we are scientifically aware! When one considers that roughly 1,000 known bird and mammal taxa are presently endangered, as many as 25,000–30,000 plant species are considered endangered or "dangerously rare," and probably comparable proportions of the other major taxonomic groups are similarly threatened, the magnitude of the impending genetic losses of this century becomes easy to comprehend.

Although it is often stated that extinction is a natural biological process that humanity has only been facilitating, in actuality there is nothing natural about the man-induced rates of extinction of recent times. One need only to consider the great Cretaceous extinction of the dinosaurs—a burst of natural extinctions that occurred rather rapidly in terms of geologic time—to understand the great disparity between natural and human-induced extinction rates. Over the course of roughly 10 million years, about 120 genera of dinosaurs disappeared—a rate of one genus for every 83,333 years. Even if we conservatively assume that there were 100 species per genus, one species would have been lost every 833 years, and assuming the implausible consideration of 1,000 species per genus—at least one extinction every 83 years. At 1,000 species per 1 million years, the rate of loss of a single species would have been 1,000 years! Thus, we have earned ourselves the dubious distinction of being the only species on earth to have ever outstripped nature in the process of extinguishing unique forms of life. The greatest tragedy is that nearly all of the species that have disappeared as a result of our influence were so well adapted to their environment that their "evolutionary death" was far from imminent.

The current rate of renewable resource exhaustion associated with the rapidly accelerating pace of extinction and disruption of the remnants of the earth's ecosystems, has contributed significantly to natural resource scarcity in our times. Are gene resources and wild species, and hence the raw materials we obtain from them, becoming more scarce? In an absolute sense, the answer would have to be an unequivocal yes. The general consensus among breeders and collectors of crop plants is that a great proportion of the genetic diversity that was available half a century ago has already vanished, despite our diligent and frantic efforts in recent years to preserve what we have. We have run out of disease resistance genes for some of the most destructive pathogens that plague wheat, rice and other major crops, and we have begun to turn increasingly to materials considered inferior for breeding pur-

poses, including the wild and distant relatives of crop plants which have proved more difficult to use. Fortunately recent advances such as genetic engineering, e.g., gene splicing techniques, may soon facilitate our use of wild gene resources. However, as these wild species disappear too, we may soon have no recourse for some diseases and pests of certain crops but to rely on the more time-consuming process of inducing single gene mutations, or of otherwise artificially accelerating the evolutionary acquisition of needed adaptations. Even though we do not presently rely as heavily on wild or primitive livestock gene resources, the general plight of the rare breeds and wild progenitors of many domesticates has been well publicized.

With respect to wild species, the accelerating pace of extinction speaks for itself. Although the current rates of exhaustion of these once renewable resources do not necessarily signal increasing resource scarcity, in part due to economic substitution effects, it is obvious that the quality of the world genetic heritage is being rapidly diminished. Thus, industrialists may not experience any diminishing returns to productivity by being forced to substitute jojoba oil for sperm oil, and they may even experience increasing returns after jojoba has been genetically improved and established as a crop. However, the whaling industry (particularly baleen whaling) may never be the same. And many unique wildlife commodities will cease to appear in the marketplace in the years to come. Internationally, within the wildlife products trade, there are already numerous examples of a switch to inferior species as superior sources have become commercially exhausted or biologically extinct. Notable examples include the progressive elimination of the superior skin-producing crocodile species, which has led to the extraction of hides from inferior species as well as from a diversity of lizard, snake, and turtle species; and the impending extinction of the spotted and striped, fur-bearing cats—a predicament which has encouraged trade in furs from bobcat, lynx, ocelot, margay, and other carnivores as well as a lively business in fake, "fun" furs. Similar examples could be provided from the ornamental plant trade, the pet trade, and other wildlife-based industries. The switch to inferior species, of course, includes the use of forests for lumber products and firewood; in many areas all of the individuals of preferred economic species have already been removed, leaving only the economically inferior species, or those once (but no longer) considered useless, for harvesting. Furthermore despite the flaws of conventional indices of natural resource scarity, including their dubious applicability to sectors based on renewable resources, the only extractive industries which have shown any signs of potential scarcity are forestry and possibly fishing—the two industries based primarily on the extraction of wild, living resources.

In sum, in response to the question, "Are living resources becoming scarce?"—it is likely that the answer would be "possibly" from the standpoint of the conventional resource economist, "probably" from the worldly-wise, environmental economist, and "definitely yes" from the international conservationist who is fighting the losing battle of salvaging portions of the gene pool resources of an ever-increasing number of vanishing life forms.

Economics and Extinction: The Challenge Ahead

The issue of increasing scarcity of the world's living resources brings us to the question of the intergenerational or intertemporal equity of our present strategies for allocating renewable, but potentially exhaustible, resources. Simply, are we

allocating these scarce resources equitably between the present and all future generations of human beings? In the face of the uncertain economic consequences and irreversible nature of extinction, and the rapidly accelerating pace at which it is occurring, concern is frequently expressed that we are not adequately providing for our posterity. A common response to this charge is that future generations will inherit the benefits of new technologies and accumulated capital stock, and thus we have no need to be concerned for the future of mankind. However, there are serious problems associated with this optimistic view of the future:

- Only a very small proportion of the raw materials extracted from the earth is presently being channeled into the production of long-term capital assets for the future;
- There is no guarantee that the technologies and economic substitutes which must be devised to replace what we now destroy will be made available when they are needed;
- Technological change is not costless, and the potential for future solutions for dealing with these costs may be diminishing rapidly due to present rates of resource depletion and environmental degradation; and
- Technology cannot recreate a species that has been lost, or "save" a species that has been reduced to a few breeding individuals; nor can it restructure a natural area that has been severely altered or degraded in terms of its biological complexity.

Recognition of these problems and concern for the welfare of future generations should lead to the conclusion that much more needs to be done to conserve the world genetic heritage and to halt the continuing degradation of the earth's remaining natural environments. Yet, it does not imply that we *must* conserve everything, for that is a practical impossibility. There are wild species and gene resources we, collectively, will choose to let go, and those so highly valued that we will endeavor to conserve them at all costs. To the extent that we develop guidelines for making rational decisions regarding the use and allocation of these resources for the benefit of all the people, the situation will inevitably improve. If we do nothing or if we fail, decisions will continue to be made in a haphazard, ill-informed, misguided, and often self-serving fashion, and the condition of mankind will continue to worsen.

We are urgently in need of a change in our collective attitudes and ethics regarding the use of our lands, waters, and biotic resources. Public concern and awareness is the crux of the solution. People must be made aware that:

- Rare, endangered, and obscure species or gene resources can provide goods and services that can be used to increase economic productivity and reduce production costs;
- Genetic improvement of preferred economic species and the location and development of novel renewable resources is one of our best economic options for reducing costs and increasing revenues for the multitude of industries which depend on biological resources;
- Without certain wild species and endangered gene resources, many of the goods and services we currently enjoy would not be available for us;
- The plant, animal, or microbe we currently employ for a particular economic purpose may not be the best or only one available;
- We have barely scratched the surface of the plant and animal kingdoms in our technological search for potential uses of living resources;

- Extinction is irreversible and it can have far-reaching and sometimes disastrous economic consequences, and whenever possible, we should err on the side of conservation when a proposed development is likely to result in extinction or irreversible environmental damage;
- The purchase of a single individual or product of a poached, endangered or rare species encourages the direct determination process;
- The economic benefits which accrue from *in situ* conservation are usually diffused among many people and are seldom acknowledged in benefit-cost analyses; as a result the true economic value of preserved natural areas is usually underestimated and indirect extermination of valuable wildlife populations therefore continues.

The key to our future, and that of our children and grandchildren, lies within our own hands. By acting now and being receptive to the problems and potential solutions, there will be much more hope for the future. However, if we continue to ignore these problems and their possible solutions, the future of mankind and that of the other inhabitants of the earth will look increasingly grim.

10

Conclusions: Effecting Global Conservation

The self-reproducing capacity of living systems is what allows biological resources their renewability, and hence, their value as potentially inexhaustible economic resources. Environmental forces ultimately direct or influence changes in the type, diversity, and quantity of genetic materials contained within living organisms; or they may alter the expression of genetically determined traits. However, only the heritable portions of these traits—the genes enclosed within the contents of living cells—can be appropriated for our use. As such, the concealed genetic material contained within a single organism, a population, or an entire species may embody a unique resource which can transcend the ephemeral existence of any human being.

Living resources, and the genes which perpetuate them, are therefore renewable resources of intergenerational significance. As long as they are properly conserved, genetic materials can be transferred from one generation to another, and their economically useful products and services can be employed to sustain social and economic systems for us and our posterity. Only through conservation can we maintain these living resources—resources that have provided us with such essential economic goods as disease-resistant crops and livestock; complex chemical compounds used in medicine and industry; timbers, fibers, and other structural materials; and energy-producing substances, such as wood, plant oils, and other hydrocarbons.

The world genetic heritage currently available for our use accumulated slowly over billions of years as a result of the gradual accumulation of genetic changes in natural populations and the acquisition and transfer of this assemblage of materials across many human generations. Yet today, we can extinguish a unique gene resource or an entire species within a single day or year. The currently rapid attrition of the resources which constitute this immensely valuable heritage is probably the major factor contributing to natural resource scarcity today. Once the self-renewing

capacity of a gene pool resource is destroyed, we cannot recreate it. And each time a living resource is irretrievably lost, we further impoverish the genetic wealth which must be conserved to protect the future of mankind as well as our own survival.

Modern society has failed to adequately integrate conservation—the wise use of natural resources—with economic development. In part this is due to the widespread and mistaken belief that conservation necessarily impedes technological progress and the contributions to human welfare which constructive development can provide. Yet after centuries of population expansion, land conversion, and technological advancement, we have finally reached the point where a failure to conserve, rather than a failure to develop, is impeding economic progress. We advocate development projects which are needlessly destructive of our irreplaceable natural resources; and we support inflexible development decisions which continue to ignore the true economic value and intangible social values of natural areas and the genetic resources they harbor. In the few instances where alternative benefit-cost analyses have been conducted, a frequent conclusion is that conservation should be the preferred alternative. Yet for the most part, these studies have not been considered, much less heeded. In a world where much of the most energetically and ecologically productive lands and waters have already been destroyed, transformed, or otherwise modified by man, we should place a premium value on the scattered remnants of the natural areas and ecosystems which remain, and on the survival of disappearing species.

Clearly, we cannot allow the massive genetic losses now taking place to continue without severely weakening the natural life-support systems that sustain the biotic foundations of every major economic sector of our society. Nor can we, in the face of so much genetic erosion, continue to depend on the genetic integrity of a mere handful of economic species, e.g., wheat, corn, cattle, *Hevea* rubber, and on our questionable capabilities to control the environmental stresses to which they will forever be vulnerable. There is much that we need to accomplish, and appropriate mechanisms for conserving the world genetic heritage must be implemented *now*. The earth's capacity to support mankind is being irreversibly diminished worldwide, the biotic resource base of our major industries is being rapidly eroded, and the costs of providing energy and other goods and services are consequently increasing. Yet society still lacks much of the necessary administrative and legislative capacity to conserve both unique and representative samples of natural areas and our accumulated genetic wealth. We are failing to adequately conserve our most economically valuable natural resources. Moreover, we have not been providing sustainable, conservation-based development options for the developing regions where they are most urgently needed.

In order to better prepare ourselves for the pressing task of effecting national and global conservation of our genetic heritage and of achieving a comprehensive and coherent program to facilitate the use and preservation of renewable biotic resources, the United States should:

- Support global gene resource conservation efforts;
- Implement a national gene resource conservation program;
- Strengthen extant conservation legislation;
- Convene national conferences to bring together people from government, industry, conservation organizations, and the scientific community, as well as interested citizens for purposes of achieving these conservation aims; and
- Institute a public education program.

Support Global Conservation Efforts

Essential groundwork needed for the development of an effective international program for conserving the world genetic heritage has already been laid. Such a program is needed to achieve international cooperation in order to conserve the world's species and gene pool resources, the vast majority of which reside in the tropics. The World Conservation Strategy—the combined effort of the IUCN (International Union for the Conservation of Nature and Natural Resources), UNEP (United Nations Environment Program), WWF (World Wildlife Fund), and FAO and UNESCO (the Food and Agriculture Organization of the UN and the UN Educational, Scientific, and Cultural Organization) (IUCN-UNEP-WWF, 1980)—provides a comprehensive and coherent program to:

- Maintain essential life-support systems and ecological processes;
- Preserve the great diversity of genetic materials contained in living organisms; and
- Ensure sustainable development and utilization of natural areas and their living resources.

This project deserves the full support and participation of the United States, and the major goals and recommendations of the World Conservation Strategy should be incorporated as objectives within a national program for gene resource conservation.

At the present time, two major international conservation organizations are coordinating and implementing gene conservation efforts worldwide. These should be used as models for the development of other *in situ* and *ex situ* gene resource conservation programs.

UNESCO-MAB (Man and the Biosphere) Programme:

The biosphere reserves program (Project No. 8) provides a vehicle for international, *in situ* conservation of:

- Terrestrial and aquatic ecosystems and natural areas;
- Traditional agro-ecosystems (areas of indigenous, subsistence agriculture);
- Other man-modified areas which enhance and maintain useful genetic diversity; and
- Research natural areas to facilitate basic ecological research on the structure and function of ecosystems, and to allow applied research on the effects of various environmental modifications.

IBPGR (International Board for Plant Genetic Resources):

This decision-making body of the Consultative Group on International Agricultural Research (CGIAR) develops programs and recommends policies to facilitate *ex situ* conservation of plant genetic diversity. Its objectives are:

- To develop an international network of plant genetic resources;
- To further the collection, documentation, conservation, evaluation, and use of these resources in order to enhance the quality of life and economic welfare of all the world's peoples;
- To establish collection priorities for endangered crop germplasm resources and to facilitate needed exploratory expeditions; and

- To promote training activities, technical meetings, and education and information dissemination in order to meet these objectives.

Appropriate international organizations should also be developed for worldwide, *ex situ* conservation of animal and microbial gene resources. The United States should provide financial assistance for and participate fully in both the UNESCO-MAB and IBPGR conservation programs.

Implement A National Program for Gene Conservation

In order to promote national and regional conservation of gene pool resources within the United States, we need a comprehensive national program. A National Council on Gene Resources has been formed in conjunction with the Gene Resource Conservation Program of the state of California. The objective of the Council is to provide information and assistance to more effectively manage, conserve, and utilize the gene resources needed by our society. It is an information-gathering and disseminating organization that links together a network of individuals representing various government agencies, conservation groups, industry, and the scientific community. At the present time, there are no funds to either support or expand the activities of the Council; since there is a great need in the United States for the services of such a council, funding should be provided to support and further its activities.

The germplasm resources and wild species indigenous to the United States are or could be used to support the productivity of various economic sectors. These resources are national treasures that are sequestered within natural areas (parks and reserves), cold storage facilities, plant introduction stations, zoos, arboreta, botanical gardens, aquaria, industrial and academic collections, private research institutions, and a great variety of other facilities that collect or maintain species, populations, collections of organisms, and specific genetic materials. The Committee on Germplasm Resources of the National Academy of Sciences has reviewed the status of these resources and of the agencies and institutions responsible for their conservation and maintenance. The Committee concluded that the United States should formally acknowledge genetic diversity as an essential national resource—a resource that is being eroded and irretrievably lost at an accelerating pace as a result of certain human activities. It recommended the formation of appropriate agencies and the provision of necessary funds to:

- Implement both national and international conservation programs;
- Enable the collection, documentation, evaluation, and conservation of our national gene resources, and the training of personnel needed for the essential task of preserving various types of biotic resources; and
- Support needed research on natural ecosystems and aspects of the use and conservation of gene resources.

Moreover, the Committee recommended a greater commitment to:

In situ conservation of:

—Natural ecosystems and communities of wild species;

—Traditional agro-ecosystems; and

Ex situ conservation of:
—Gene resources of economic plants, animals, and microbes;
—Genetic stocks of research organisms; and
—Populations of nonhuman primates needed for biomedical research.

Strengthen Extant Conservation Legislation

In an attempt to halt the accelerating pace of extinction within the United States, and to encourage federally funded development projects to consider the social, economic, and other benefits which our biotic resources provide for all the people and our posterity, the U.S. Congress has enacted appropriate conservation legislation and treaties. However, most of these should be strengthened in order to promote the objectives of global and national conservation of our genetic heritage, specifically the:

- NEPA (National Environmental Policy Act of 1970) should be amended to:
  —Include consideration of the potential adverse impacts of proposed projects on genetic materials and wild species determined to be of special socioeconomic interest as national resources; such a list could be developed as part of the mandate of a national program for gene conservation.
  —Include an emphasis on the impact of proposed developments on the *natural* environment as well as the *human* environment, especially to the extent that it will facilitate protection of our national genetic heritage.
  —Impose substantive, legally enforceable standards of environmental quality on decision-making processes in order to protect the genetic heritage.
  —Extend the provisions of the Act to include federally funded projects conducted in foreign environments.
- Endangered Species Act of 1973 (as amended through 1982) should:
  —Continue indefinitely after fiscal year 1982.
  —Be made into a *workable* program for the preservation of endangered species as well as distinct endangered populations (subspecies, varieties) of biological resources deemed to be of national importance.
  —Be amended to correct inequalities which exist for plant species, especially sent there are no prohibitions on the taking or removal of endangered (listed) plants from privately-owned lands, whereas threatened (listed) taxa of fish and animal wildlife are so protected.
  —Provide for special funds to assist the listing process and acquisition of habitat for preservation of endangered resources which form part of our national genetic heritage.
- Lacey Act of 1900 (as amended through 1981) should be amended to:
  — Expand its scope to regulate importation of exotic plant species taken or possessed in violation of foreign laws.
- *CITES* (Convention on International Trade in Endangered Species of Wild Fauna and Flora) should be facilitated by appropriate amendments to the U.S. Endangered Species Act and the Lacey Act which would:

—Increase funds needed to enforce CITES regulations both internationally and nationally.
—Increase both civil and criminal penalties for CITES infractions in the United States.

Convene National Conferences

In order to facilitate the exchange of ideas and information regarding aspects of the use and preservation of our genetic heritage, a national conference was held in Washington, D.C. in November 1981. The U.S. Strategy Conference on Biological Diversity, sponsored by the U.S. Department of State and Agency for International Development, brought together experts from various government agencies, private foundations, academic and research institutions, conservation groups, and industries to assess the socioeconomic importance of biological resources to the United States and the world, and the potential consequences of impending losses of biological diversity to humanity. The major conclusions and recommendations of the participants of the U.S. Strategy Conference should be heeded. Additionally, necessary funds should be provided for follow-up conferences which will be needed to amass and disseminate information about the potentialities for utilizing biological diversity to enhance economic productivity and social welfare, and our options for conserving our genetic heritage. Collection of such information could also serve a dual purpose by facilitating the development of a national program for gene resource conservation and the establishment of a U.S. Interagency Task Force for conservation of biological diversity.

Institute Public Education Programs

The public must be made more aware of the contributions of genetic materials and wild species to economic productivity and our society in general, as well as of the socioeconomic consequences of irretrievable losses of these renewable resources. The tangible economic values of many hidden genetic materials and obscure wild species are as difficult to perceive as are many of the economic goods and services they offer. Thus, most people do not have sufficient information to understand the impact that these national treasures can have on their daily lives. Exhibits should be provided in promiment public places, e.g., in the lobbies of government buildings, national, state, and local museums and research institutions, USDA research facilities, and the visitor centers of national and state parks. A national poster campaign is another option that could be explored to provide information about the socioeconomic value of particular gene resources, or possibly to promote citizen involvement in the enforcement of CITES and the U.S. Endangered Species Act. For example, colorful, artistic drawings or black and white photographic displays of commonly traded but protected endangered species and their derived products could be displayed in post offices and other public places. In concert with a national educational campaign about the societal values of preserving endangered species and gene resources, such posters would alert the public about especially valuable or threatened species.

Genetic resources, and the wild or domesticated species and populations from which they are obtained, are indeed national treasures which can and should be dis-

covered, appreciated, and enjoyed by the people of our nation. Through international and national cooperation, federal protection, and public education, we can maintain a vast and genetically rich heritage of living resources for all Americans and our fellow human beings, and provide the means to conserve this heritage for future generations.

Appendix—Types of Genetic Resources

Plant and animal resources are often described in terms of the degree to which they have been genetically improved, i.e., wild, weedy, or domesticated. Wild plant and animal species, which have not been improved, typically do not survive well in cultivated or disturbed habitats; they thrive only so long as the natural conditions of their essential habitats are maintained *in situ*. Weedy plant (and animal) species are often aggressive colonizers of disturbed habitats, and many acquire this capability via natural crosses with related domesticates. Weeds typically do not require artificial maintenance, since most can establish new populations within disturbed habitats without man's help. Although they will thrive in disturbed habitats, weedy species are gradually replaced by a succession of wild species once the habitat is no longer disturbed. Domesticates, on the other hand, must be cultivated or maintained artificially within a manipulated habitat. Nearly all of them have lost their ability to survive without the aid of man through many centuries of genetic improvement and human selection for adaptation to our manipulated agroecosystems.

Wild and Weedy Genetic Resources

Wild and weedy biota provide natural sources of useful commodities, since they arose and are maintained without any necessary assistance on the part of man. Many of these gene resources are currently economically valuable to us, either directly or indirectly. Some have provided us with edible nuts, fruits, vegetables, spices, oils, and so on. Additionally, relatives of crop species are frequently used as valuable sources of disease or pest resistance or other adaptive traits for modern crop cultivars. In some cases, these genetic materials are our only known sources of such economically useful characteristics. Besides their direct value, wild flora and fauna may be used to enhance the productivity of other species. Agricultural productivity

has been increased by using improved forage or range grasses for pasturing livestock, plants for the reclamation and conservation of agricultural soils, and various species of draft animals, insect pollinators, and biological control organisms which serve in the food production process. Similarly, a variety of wild plants and animals are crucial in the development, evaluation, and testing of medicinal drug compounds.

Many wild and weedy species were important in the past and may again be useful to us once we perceive new values or uses for them. We will also discover novel uses for other wild biota or weedy plants. Trends we have already experienced in resource use demonstrate that human values, desires and needs change radically over time. For example, many edible plants which were once staple foods for previous civilizations are no longer employed at all for food production, or they have only recently been rediscovered as uniquely valuable food items.

The substitution of once utilized resources for newly discovered ones has accelerated in recent times, paralleling the combined effects of increases in human population, new technological innovations and biological discoveries, and more lately, the extinction or depletion of economically exploited genetic resource species. These trends will undoubtedly continue, even though the latter phenomenon—the irrevocable loss of certain genetic resources—is a self-defeating trend.

Gene pools of wild and weedy biota are best conserved *in situ*—within their natural environments or their original habitats. Natural ecosystems serve as our primary reservoirs of genetic diversity for wild resource species, yet human-disturbed habitats—particularly those closely associated with traditional agro-ecosystems—are prime areas for conservation of many weedy species. Therefore, we should conserve a broad range of natural environments for wild gene resources and a few, select man-disturbed habitats for some weedy relatives of crops; however, most weedy species can easily be conserved along roadsides, railroad rights-of-way, and other such disturbed habitats.

Primitive Crop Cultivars and Livestock Breeds

Primitive or landrace crop cultivars are commonly associated with premodern peoples, primarily those who use traditional farming methods or practice subsistence agriculture. These concepts of primitive crop cultivars can be applied as well to primitive or landrace breeds of livestock. Landrace breeds are often, and perhaps more accurately, called native breeds or rare breeds, although the latter term actually reflects their conservation status rather than any inherent characteristic of such gene pool resources. Native animal breeds have similarly acquired unique adaptations in response to the special needs of their domesticators and the selective pressures within the environment in which they originated. Many economically useful genetic traits can be transferred from them to more highly productive, advanced breeds of livestock by cross-breeding.

Ideally, primitive genetic resources are best conserved in their original habitats. *In situ* conservation would allow these resources to continue to be influenced by the natural selection pressures of their environments, particularly the constantly evolving populations of their native diseases and pests. However, in many instances, *in situ* conservation options are politically or socially impracticable. Therefore, various *ex situ* conservation strategies must be employed frequently instead in an attempt to

preserve representative samples from their gene pools as well as to maintain very rare cultivars or breeds which are in danger of extinction.

Advanced Crop Cultivars and Livestock Breeds

Genetic resources developed or significantly improved by modern scientific breeding techniques are termed advanced. In comparison with primitive cultivars and breeds, advanced or modern cultivars and breeds have generally been subjected to more intense artificial selection. Advanced crop cultivars have been the most widely used genetic resources in crop improvement programs; recently, however, as useful disease and pest resistance genes have been exhausted from these sources, plant breeders have turned increasingly to primitive cultivars and wild relatives for these and other important heritable qualities lacking in advanced stocks. Modern crop cultivars are indispensible genetic resources; yet by themselves, they provide a very narrow base for crop improvement programs.

Advanced livestock breeds are today used almost exclusively in industrialized nations, though some modern breeds, such as the Santa Gertrudis cattle, originated from crosses between improved British breeds and landrace breeds of cattle. In many cases, advanced breeds are highly inbred genetic strains of livestock, (e.g., Holstein, Hereford), just as most advanced crop varieties are genetically homogeneous in comparison to the primitive cultivars or wild species from which they were obtained. Their productivity or yield performance is well-documented; however, their genetic uniformity has often rendered them susceptible to disease and pests and ill-adapted to certain climatic conditions. In addition, many advanced crop varieties lack the nutritional value of their primitive or wild relatives (gram for gram), as well as some important culinary, flavor, and storage properties.

Advanced genetic resources are best conserved by various *ex situ* conservation methods, particularly by cold storage of crop seeds and maintenance of distinct genetic stocks of modern breeds. Resources conserved by *ex situ* methods are usually more readily available to breeders for use in genetic improvement programs. When an advanced cultivar or breed has been superceded by other genetic lines, it is termed obsolete. Many of the now rare, native breeds of livestock fall into this category. Others have been genetically improved since the advent of modern plant or animal breeding techniques, yet they are no longer directly utilized for crop or livestock production.

In addition to losses of rare cultivars and breeds during the last century, many obsolete but important cultivars and breeds have also disappeared. Although cost and space limitations prevent every obsolete stock from being maintained *ex situ*, such losses can be most unfortunate. Aside from their potential breeding value due to their status as relatively improved economic resources, obsolete cultivars and breeds possess historical value, and they can provide clues to the recent evolutionary histories of preferred breeds or crop varieties. Obsolete, advanced stocks often harbor useful heritable traits which, in comparison with more primitive genetic resources, can generally be more easily transferred to currently important advanced cultivars or breeds.

Stocks Improved by Induced Mutations

When combined with artificial selection, controlled reproduction, and other common means of manipulating variability within genetic resource populations, induction of mutations, e.g., by X rays or chemical mutagens, can also contribute to the plant improvement process; but such methods cannot be employed for improvement of domestic animals (with the exception of microorganisms). Over 100 crop varieties have been improved by induced mutations, and artifically induced mutations are likely to be used more frequently in the future as our natural genetic reservoirs continue to disappear. However, in comparison with traditional sources of plant-breeding materials from natural and man-modified environments, induced mutations have, thus far, contributed insignificantly to the crop improvement process.

Glossary

adaptation—a genetically determined trait that enhances an organism's ability to cope with its environment.

adaptive trait—see **adaptation**.

advanced cultivar or **advanced breed**—a crop cultivar or livestock breed that has been improved significantly by modern breeding techniques, and that is generally ill-adapted for survival in the wild. It is typically higher-yielding in an intensively managed (modern) agro-ecosystem, and morphologically distinct from a primitive cultivar or breed.

agro-ecosystem—a man-modified ecosystem consisting primarily of domesticates cultivated or husbanded and managed by man, and a physical environment suitable for the propagation of individuals of such species. In most cases, they are partly supported by nearby natural ecosystems which contribute nutrients, water, biological control agents, or other essential elements.

allele—one of two or more alternative forms of a gene. Mutations give rise to different alleles at the same gene locus.

alkaloid—any of a large group of nitrogen-containing, organic compounds most commonly found in seed-producing plants and in herbivorous animals that feed on such plants. Alkaloids are typically biologically or pharmacologically active.

angiosperm—a "higher" or flowering plant which produces seeds enclosed within an ovary; a plant or species belonging to the class Angiospermae of the vascular or land-dwelling plants (division Tracheophyta).

artificial selection—selection applied according to a specified set of environmental conditions. In contrast to natural selection, it is a purposeful process directed by man (usually a plant or animal breeder) in order to meet certain socioeconomic goals or standards; see **selection**. (Compare **natural selection**.)

biological productivity—see **primary productivity**.

biology—the science of life; the study of the principles applied to the origin, structure, function, development, and ecology of living organisms as represented by plants, animals, and microbes.

biomass—the total weight of living material, usually expressed in terms of dry weight of an organism, a population, or a community.

biota—flora and fauna, considered together.

biotoxin—a naturally produced, toxic compound which shows pronounced biological activity and presumably has some adaptive significance to the organism which produces it; biotoxins are often pharmacologically active, and they are ultimately produced as a consequence of gene action.

breed—a group of domesticated animals genetically related by descent from common ancestors and which share similar phenotypic characteristics.

breeding—the propagation of plants and animals, especially for the purpose of genetically improving particular cultivars or breeds through artifical selection and incorporation of genetic materials acquired as a result of natural selection pressures.

carnivore—see **predator.**

cell—the fundamental structural and functional unit of all living matter.

chromosomal aberration—any change in chromosome structure or chromosome number. Although it can be a mechanism for enhancing genetic diversity, such alterations are usually fatal or ill-adaptive, especially in animals.

chromosome—self-duplicating units of genetic material which are species-specific in number and complexity (and often organism-specific in cases of chromosomal aberrations).

chromosome set—see **genome**.

coadaptation—genetically, the evolutionary process of selection for harmoniously collaborating genes within the gene pool of a population; genes are coadapted if the specific interactions between them confer high fitness to the individual inheriting them. Ecologically, the evolution of mutually advantageous heritable characteristics within two or more species as a consequence of their ecological interactions over time.

coadapted gene complex—a mutually concordant set of alleles (genes) that, when inherited intact, confers fitness to the individual; although they need not be closely linked on the same chromosome, the alleles that comprise such a complex have been most often demonstrated to exist in tightly linked systems inherited as a unit.

coevolution—the joint evolution of two (or more) taxa resulting in the mutual development of genetically determined traits, advantageous to each other, that facilitate their ecological interactions; even though coevolved species have close ecological relationships, they do not exchange genetic material with one another.

common property resource exploitation—the harvesting process by which a commonly owned resource (public good) is extracted for socioeconomic purposes by as many users or harvesters as can be supported by the resource base, under the constraints of market demand and degree of access to the harvesting grounds; since a public good is owned by no one in particular and access is usually open to common harvesting grounds, a biotic resource is especially vulnerable to depletion or extinction whenever market demand is high. (Compare **open-access exploitation.**)

community—the biotic components (all organisms considered together) in an ecosystem; an association of interacting populations.

competitor—a species (population) that uses or defends a resource, thus reducing its availability for use by another species (population).

conservation—the wise use of natural resources; the planned management of a natural resource to deter or prevent overexploitation, irreversible destruction, or neglect.

crop gene center—a region or center of pronounced genetic diversity for a crop species which arose in association with traditional agro-ecosystems and ancient farming practices; primary = a site where crop species were first domesticated and became genetically diversified, and secondary = an area of pronounced genetic diversity of a crop which did not originate there.

crossbreeding—see **outbreeding.**

cryobiological preservation—the preservation of germplasm resources in a dormant state by cryogenic techniques, as currently applied to banking of plant seeds and pollen, microorganisms, animal sperm, and tissue culture cell lines. (Compare ***ex situ*** **conservation**.)

cryogenics—the branch of physics relating to the effects and production of very low temperatures; as applied to living organisms, preservation in a dormant state by freezing, drying, or both.

cultivar—a cultivated variety (genetic strain) of a domesticated crop plant.

deforestation—extensive removal or clearing of the primary vegetation of a forest (or woodland), usually resulting in a substantially reduced standing biomass, biotic impoverishment, destruction or disturbance of ecological interactions, and sometimes more permanent or irreversible effects such as laterization of soils.

desertification—the process by which a semi-arid or other ecologically fragile environment is transformed into a desert or barren tract of land. It is often human-induced through extensive removal of extant vegetation or overuse of water resources by man or domesticated animals.

discount rate—the rate that determines the present monetary value of future benefits that will accrue from an investment, or a measure of revenue or income that will be lost through receipt of monetary returns in the future rather than now; high discount rates tend to inhibit conservation and facilitate development of natural environments.

domesticate—a domesticated animal or plant species; an individual of a species that has evolved in intimate association with man and that after many generations of artificial selection, protection, and nurturing by man, has acquired phenotypic traits which serve man's needs yet which so distinguish it from its wild ancestors that it can no longer survive without human intervention.

dominant allele (trait)—an allele that masks or overrides the expression of an alternative allele (trait) when both are present in the same genotype (cell or individual). (Compare **recessive allele**.)

ecology—the science or study of the relations and interactions among organisms as well as with their physical environment.

economic good—a resource that is scarce because of finite or limited availability, and which must therefore be allocated among competing uses or concerns. (Compare **free good.**)

economic productivity—the production or provision of economic goods and services through the employment of capital and labor (production factors) and the exploitation of "free goods" provided by nature. On a national scale, it is

often collectively measured or monetarily evaluated by such economic indicators as GNP (Gross National Product), NNP (Net National Product), or NEW (Net Economic Welfare). (Compare **primary productivity**.)

economics—the study of how men or their societies choose various methods of using scarce, productive resources and of allocating them among competing uses or applications or over generations of humanity (i.e., intergenerationally).

ecosystem (natural)—the sum total of the living (biotic) and nonliving (abiotic) components of a particular environment.

electrophoresis—a technique which can be used to detect phenotypic variation by separation of different proteins (gene products) contained in blood serum or living tissues on the basis of differences in their net electrical charges.

endangered (taxon)—a species, subspecies, or distinct population in immediate danger of extinction.

environment—the surroundings of an organism, including the other organisms with which it interacts.

evolution—a change in the genetic make-up (allele frequencies) of a population over time; see **genetic diversity**.

***ex situ* conservation**—a conservation method which entails the actual removal of germplasm resources (seeds, pollen, sperm, individual organisms) from their original habitat or natural environment; see **gene bank, mass reservoir, genetic drift**. (Compare ***in situ* conservation**.)

external benefit (external economy)—a benefit resulting from a particular economic activity which a party other than the producer receives free-of-charge, e.g., the owner of a residential development benefits from an increase in property values when an adjacent property owner decides to convert his land to a recreational park.

external cost (external diseconomy)—a cost resulting from a particular economic activity which is borne by society or someone other than the producer, e.g., a coastal fishing industry goes out of business because industrial pollution and coastal development operations destroyed nearby estuaries (breeding grounds for fish populations).

externality—see **external benefit** and **external cost**.

extinction—the human-induced or natural process whereby a species, subspecies, or distinct population ceases to exist. (Compare **conservation**.)

fitness—the relative proportion of an individual organism's genes that remain in the gene pool of its population; the genetic contribution of an individual's descendents to future generations of the population.

flowering plant—see **angiosperm**.

food web—a representation or diagram depicting the paths of energy flow occurring among the various populations or species in a community.

free good—in theory, an infinitely available good or commodity that need not be allocated among users since it is an unlimited or a natural resource; in practice, a natural resource, including pure air or water, or a species or natural environment, is not an unlimited or infinitely available resource. (Compare **economic good**.)

gamete—a mature reproductive cell (sex cell) which carries a single genome, and which fuses with another reproductive cell during fertilization in order to produce a new individual; in animals, an egg or a sperm.

gene—the functional and structural unit of inheritance; each gene is located in a particular region of a chromosome (gene locus), and contains the genetic information necessary to encode all or part of a protein, or to perform some regulatory function.

gene bank—a facility established for the *ex situ* conservation of individuals (seeds), tissues, or reproductive cells of plants or animals by cryobiological preservation techniques.

gene conservation or genetic resource conservation—the conservation of species, populations, individuals, or parts of individuals by *in situ* or *ex situ* methods to provide a diversity of genetic materials for the socioeconomic needs of present and future generations.

gene pool—the sum total of all the genetic information encoded within all the genes of a breeding population. (Compare **germplasm**.)

generalist—a species that exhibits a broad habitat or feeding preference, or both. (Compare **specialist**.)

gene or genetic resource—the socioeconomic use and value of the genetic materials (information) contained within living organisms or within the gene pool(s) of their population(s); see **genetic diversity**.

genetic diversity—the heritable variation within and among populations which serves as the source of genetic resources, and which is created, enhanced, or maintained by evolutionary forces (see **mutation, migration, selection,** and **genetic drift**) or gene reshuffling processes (see **recombination** and **mating systems**).

genetic drift—an evolutionary force that results in changes in allele frequencies within a population due to chance or random variations in births or deaths; since drift is thought to be diversity-reducing, it can result from the random sampling or from extermination of individuals within a population, and is therefore an important consideration for gene conservation.

genetic erosion—the process by which genetic resources are destroyed or irretrievably lost by the extinction of species, populations, or loss of specific germplasm resources, or by failure to maintain *ex situ* conserved germplasm resources.

genetic improvement—genetic alteration of a population of an economically important species to meet certain socioeconomic needs or to achieve some level of performance or adaptation; see **breeding**.

genetics—the science or study of heredity and genetic variation.

genome—a single, complete chromosome set within an organism; in humans and other higher animals, somatic cells contain two genomes (diploid) while gametes or reproductive cells contain a single genome (haploid).

genotype—all of the organism's genetic characteristics that influence or determine its structure and function. (Compare **phenotype**.)

germplasm—the genetic material, especially its specific molecular and chemical constitution, that comprises the physical basis of the inherited qualities of an organism; it can be transmitted to future generations by reproductive cells (gametes) or by vegetative (asexual) reproduction. (Compare **gene pool**.)

germplasm resource(s)—a genetically determined trait of economic significance, an individual that carries such a trait, or a collection of such individuals.

habitat—the specific place where a plant or animal usually lives, often designated by some physical characteristic or by a dominant plant type.

herbivore—see **predator**.

heredity—the transmission of genetically determined traits from parent organisms to their offspring.

heritability—the proportion of variance in a phenotypic (observable) trait that can be attributed to the additive effects of genes rather than the environment; see **genotype, phenotype**.

heterosis—the superiority of crossbred offspring, i.e., those derived from crosses between genetically unlike or different individuals or those with different alleles at the same gene loci (as compared with offspring from these individuals when crossed with mates that have the same alleles at the respective gene loci); see **mating system, outbreeding, inbreeding**.

higher plant—a vascular, seed-producing plant; see **angiosperm**.

hybridization—crossbreeding between two genetically dissimilar individuals, resulting in the production of hybrid (crossbred or outbred) progeny which sometimes exhibit heterosis.

hybrid vigor—see **heterosis**.

inbreeding—a mating system involving the mating or breeding of closely related individuals, the most extreme form of which is self-fertilization; it is used to "fix" economically useful genetic traits in genetically improved populations, however it also can result in fixation of deleterious recessive alleles; see **inbreeding depression**. (Compare **outbreeding**.)

inbreeding depression—a reduction in fitness or vigor as a result of fixation of deleterious, recessive alleles from consistent inbreeding in a normally outbreeding population; see **fitness, heterosis, inbreeding**.

induced mutation—a mutation artifically induced by radiation, chemicals, or some other mutagenic agent; see **mutagen, mutation breeding**.

inheritance—see **heredity**.

***in situ* conservation**—a conservation method that attempts to preserve the genetic integrity of gene resources by conserving them within the evolutionary dynamic ecosystems of their original habitat or natural environment. (Compare ***ex situ* conservation**.)

intergenerational equity (intertemporal equity)—the economic issue of how to equitably allocate scarce resources among present and future generations, especially with concern to the biases inherent in current economic decisions due to lack of representation in the marketplace of future consumers; it is of particular interest in cases where irreversible resource commitments are made by the present generation, e.g., extinction of species or the complete transformation (destruction) of a natural environment.

internal rate of return (IRR)—the rate that determines the marginal efficiency (internal profitability) of a particular investment project. It equilibrates the immediate cost of the project with the discounted present value of expected (future) net returns from the project; see **discount rate**.

interspecific—between or among species (herein, it is used broadly to indicate differences at all higher taxonomic levels above the species level as well).

intraspecific—within a species or its populations (including subspecies).

landrace— a crop cultivar or animal breed which evolved with and has been genetically improved by traditional agriculturalists, but has not been influenced by modern breeding practices; see **primitive cultivar or breed**.

larva (plural = larvae)—an immature, wingless form of many insect species (and some other animals) which undergoes a radical transformation (metamorphosis) to attain adult size and form.

laterization—an alkaline soil reaction precipitated by extensive leaching (removal by rainfall) of silica from the soil. Usually, it occurs in moist, tropical regions, and can result in the irreversible (or nearly so) hardening of soil into rocklike formations following extensive vegetaticn removal; see **deforestation**.

mass reservoir—an *ex situ* conservation strategy characterized by introduction of a wide array of gene resource stocks, including wild, primitive, and advanced types, into a suitable area in order to facilitate the development of locally adapted crop genotypes via selection among the offspring of crosses between these diverse types of resources. They can provide reservoirs of breeding stocks for some crops, and therefore may be used as a partial substitute for our genetically diverse, but rapidly disappearing primitive landrace varieties of crops; see ***ex situ* conservation.** (Compare **gene bank.**)

mating system—the mating patterns that naturally occur among individuals within a breeding population, including degree of inbreeding or outbreeding, number of mates chosen during a breeding season, permanence of pair-bonding, etc; see **inbreeding, outbreeding.**

microorganism (microbe)—a microscopic organism, either plant or animal, but usually a protozoan, bacterium or virus.

migration—an evolutionary force which causes changes in allele frequencies due to interpopulational movements, by individual organisms moving into a particular population (immigration) or out of it (emigration). It results in gene flow (a flow of genes from one population's gene pool to another's), which can enhance genetic diversity when genetically dissimilar, reproductive individuals are brought together.

modern agro-ecosystem—an agro-ecosystem characterized by high inputs of fossil fuel energy, fertilizers, pesticides, and water, and the use of high-yielding modern cultivars (or breeds) planted (husbanded) in monocultures.

modern cultivar/breed—see **advanced cultivar/breed**.

monoculture—the cultivation (husbanding) of a single crop or crop cultivar (livestock species or breed) over a wide or extensive area.

mutagen—an agent, such as radiation, ultraviolet light, mustard gas or some other chemical, which tends to increase the occurrence of mutations.

mutation—the evolutionary force that is the ultimate source of all genetic diversity and that involves any change in the original message or genetic information encoded within a gene, chromosome, or genome; the creation of a new allelic form of a gene; see **genetic diversity, evolution, mutagen, induced mutation**.

mutation breeding—a modern breeding process that principally relies on induced mutations as the source of new recessive alleles which determine the inheritance of economically useful traits; see **induced mutation, mutagen.**

natural selection—selection that occurs by natural processes and that induces evolutionary changes through differential mortality or survival of certain genotypes (individuals); see **selection.** (Compare **artificial selection.**)

nutrient cycle—the path of a nutrient or element through an ecosystem, including its assimilation and release by various organisms and its transformation into various organic or inorganic chemical forms.

omnivore—see **predator**.

open-access exploitation—use or harvesting of a resource under conditions of unlimited or free access to the harvesting grounds or area. The more open or unlimited the access, the more vulnerable the resource will be to overexploitation, whether it is publicly or privately owned; see **overexploitation**. (Compare **common property resource exploitation**.)

outbreeding—a mating system characterized by the breeding of genetically unrelated or dissimilar individuals. Since genetic diversity tends to be enhanced and since vigor or fitness of individuals can be increased by this process, it is often used to counter the detrimental effects of continuous inbreeding; see **inbreeding depression, hybridization, heterosis, mating system**. (Compare **inbreeding**.)

overexploitation (overharvesting)—the use or extraction of a resource to the point of depletion (or extinction). Biologically, it usually refers to overharvesting of a resource population to a level below the maximum needed for a sustainable yield (the level at which a population can, theoretically, continue to be optimally harvested over the long-run).

parasite—an organism that lives within (endoparasite) or on (ectoparasite) a host organism, consuming part of it or its nutrients or energy sources, but usually not killing it.

pathogen—a disease-causing microorganism; a bacterium or virus.

pest—an organism that competes with, preys upon, parasitizes, or otherwise interferes with man or his domesticated (cultivated or husbanded) biota.

phenotype—the sum total of the ecological, morphological, physiological, biochemical, and behavioral attributes of an organism during all of its life stages; the physical attributes of an organism as determined by interactions between its genotype and its environment. (Compare **genotype**.)

photosynthesis—the use of solar energy or light and inorganic precursors (water and carbon dioxide) by self-feeding plants to produce high-energy, organic compounds (simple sugars).

population—a group of individuals with common ancestry that are much more likely to mate with one another than with individuals from another such group. (Compare **species**.)

polygenic trait (inheritance)—a trait genetically expressed as a result of the action of many interacting but not necessarily genetically linked genes, each exerting only a partial influence on the phenotype.

predator—an animal (only rarely a plant) that kills and consumes (usually fresh) another animal or plant. An organism that preys on animals is a carnivore, while that which preys on plants is an herbivore; omnivores consume both plants and animals.

primary productivity—the rate of biological assimilation (gross primary productivity) or accumulation (net primary productivity) of nutrients and energy by photosynthetic (green) plants. The most productive ecosystems include reefs, estuaries, swamps and marshes, and tropical and temperate forests. (Compare **economic productivity**.)

primitive cultivar or breed—a crop cultivar or livestock breed that has been genetically improved by traditional agriculturalists and that no longer resembles its wild progenitor(s), yet that usually retains many of the beneficial genetic traits of its wild ancestors; see **landrace**. (Compare **advanced cultivar** or **breed**.)

protein—an organic compound produced by a gene or many genes; ultimately it determines some aspect of the structure or function of the organism. Proteins may serve a regulatory function, a catalytic function (enzymes), or a structural purpose; they are the principal gene products; see **gene**.

public good—a good (or service) consumed or used collectively by most people in a society or economic system, e.g., national defense equipment, roads and bridges, highly mobile animal populations, and national parks.

recessive allele (trait)—an allele (genetic trait) masked or overridden by the effects of an alternative allele (trait) when both are present in the same genotype (or cell or individual). (Compare **dominant allele**.)

recombination—any mechanism by which new genotypes are formed during the reproductive process (in a breeding population) as a result of the mixture or reshuffling of genes, chromosome segments, or entire chromosomes.

reproduction—the production of an organism or cell by one (asexual) or two (sexual) parents.

resistance (genetic)—the genetically determined capability to avoid or counter the attack of a disease pathogen or pest organism.

roguing—an artificial selection process in which individuals (especially trees) are selectively removed from a population so that only the most desirable phenotypes will be left to reproduce.

selection—an evolutionary force that shapes a population or species into a collection of biologically fit or economically ''fit'' or productive genotypes; the nonrandom, differential reproduction of genotypes; see **natural** vs. **artificial selection, fitness, evolution**.

selective force—any biotic (man, other organism) or abiotic (temperature, rainfall) factor that directs or influences the process of selection.

specialist—a species that exhibits a very narrow habitat or feeding preference, or both. (Compare **generalist**.)

species—a group of actually or potentially interbreeding individuals isolated (in a reproductive sense) from all other groups of organisms. (Compare **population**.)

taxon (plural = taxa—any group of individual organisms (recognized as a formal unit) genetically related by a common ancestor.

tissue—an aggregation of cells similar in structure and function and bound together by an intercellular substance.

tolerance (genetic)—a form of genetic resistance in which the organism is attacked or affected by a disease pathogen (or pest) and yet exhibits less reduction in yield or performance in comparison with members of other affected cultivars or breeds.

traditional agro-ecosystem—an agro-ecosystem characterized by intensive use of human labor, traditional farming practices, and technologically unsophisticated cultivation and harvesting implements, and which relies on use of primitive crop cultivars (or breeds). (Compare **modern agro-ecosystem**.)

warning coloration—the conspicuous appearance or coloration of a particular species which serves to warn potential predators that individuals of that species or taxon are noxious, distasteful, or poisonous, e.g., a pattern of orange or red on black; aposematism.

weed (species)—a species which has good colonizing (reproductive) capabilities in a disturbed environment, and can usually outcompete a wild species therein; it cannot outcompete wild species in natural environments, and since it thrives in human-disturbed habitats, it is typically considered as an unwanted, economically useless, or "pest" species. (Compare **wild (species), cultivar, breed**.)

wild (species)—a species which usually exists in and often requires an undisturbed natural habitat, and which has not been influenced by the artificial selection pressures of man. Although it can sometimes be cultivated, a wild species remains such only so long as its natural habitat is maintained. (Compare **weed (species), cultivar, breed**.)

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